LIVE LONG AND PROSPER
A THEORY FOR YIELD DIFFERENCES BETWEEN ANNUAL AND PERENNIAL GRAINS

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Abstract

Several decades of breeding efforts to produce a high-yielding, long-lived herbaceous grain have not been successful. Yet, such a plant is conjectured to have many advantages over the annual grains society uses to feed itself — advantages which are sorely needed as population growth and environmental limitations coalesce. This work lays a mathematical foundation for determining whether such a plant can ever exist and argues that it can.

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All of the variables used in this thesis are handily defined alphabetically in this table. If you're reading a loose-leaf copy of the thesis, it may be convenient to remove this page for reference later. If you are reading a bound copy... try to restraint yourself.

Symbol	Description	Unit
a	A tissue conversion rate	$\frac{g}{g \cdot day}$
$C(t)$	Competitive tissue mass	g
C_0	Initial value of C at $t = 0$	g
$g(P)$	Production rate	g/day
$g_{\max}$	Maximum production rate	g/day
K_p	Half-saturation constant of production	g
l_p	Loss rate of productive tissue	$\frac{\mathrm{g}}{\mathrm{g} \cdot \mathrm{day}}$
n	The nth growing season	1
$P(t)$	Productive tissue mass	g
P_0	Initial value of P at $t = 0$	g
R	Harvested seeds of one growing season (to be solved for)	g
S	Final storage mass in the multi-season context	g
$S(t)$	Storage tissue mass at time t within a growing season	g
S_0	Initial value of S at $t = 0$	g
t	Time within a growing season	days
T	Duration of a growing season	days
$u(t)$	Control (to be solved for)	$\in [u, 1]$
$u'(t)$	A modified control	$\in [u, 1]$
$V(S)$	Optimal reproductive value over several growing seasons	g
$w(t)$	Control (to be solved for)	$\in [u, 1]$
α	Competition coefficient	$\in (0, \infty)$
β	Competition coefficient	$\in (0, \infty)$
γ	Interseasonal tissue loss	1
μ_p	Metabolic cost of productive tissue	$\frac{\mathrm{g}}{\mathrm{g} \cdot \mathrm{day}}$
μ_s	Metabolic cost of storage tissue	$\frac{\mathrm{g}}{\mathrm{g} \cdot \mathrm{day}}$
$\psi_T(S)$	Storage value at the end for growing season of length T	1
σ	Interseasonal discount rate/survival odds	1

Time dependent variables, such as $P(t)$ may occasionally be used without time explicitly noted, as in P.

Any symbol with a dot, such as $\dot{P}$ represents the first time derivative $\frac{\mathrm{d}P}{\mathrm{d}t}$ of that variable.

Chapter 1

Outline

Several decades of breeding efforts to produce a high-yielding, long-lived herbaceous grain have not been successful. Yet, such a plant is conjectured to have many advantages over the annual grains society uses to feed itself — advantages which are sorely needed as population growth and environmental limitations coalesce. In this thesis I use ecological theory to argue that, despite the difficulties encountered, it is possible for such a plant to exist.

The thesis is organized as follows.

In **Chapter 2** I discuss agriculture, its costs, and the possibility that high-yielding herbaceous perennial grains would reduce these costs (§2.1) and present hypotheses for why such grains do not already exist (§2.2). I argue that a theory-driven approach can offer valuable insight into whether such grains can be bred (§2.3). After reviewing several modeling approaches (§2.4), I argue that the approach used here is practically, philosophically, and epistemologically preferable to alternative formulations for answering the question at hand (§2.5).

In **Chapter 3** I present my model. Initially I consider only a single plant. The model is used to find an optimal multi-season strategy (§3.1) for this plant; however, in order to determine reasonable growth parameters for the plant a second part is introduced to the model which is used to find the optimal strategy within a single growing season (§3.2). Later, I consider more complex formulations accounting for metabolism and tissue loss (§3.5), as well as competition (§3.6).

In **Chapter 4**, I consider and respond to some possible objections to the model which were not covered earlier in the thesis. Possible ways of adding complexity to the model are discussed in relation to existing works. Finally, I present my conclusions.

Chapter 5 contains a bibliography.

To ensure that the work is reproducible, the appendices contain source code and instructions for building an environment in which to run the code. My approach relies on external libraries which may not be available in the future. To counter this, where such libraries are used I try to be explicit about their function so that the concepts, at least, will endure.

Chapter 2

Background

2.1 Agriculture & Perennial Grains

Compared to the large harvests of seed produced by annual grains, herbaceous perennial grains yield far fewer seeds. [51, 58, 61] While natural selection has not produced an herbaceous grain that combines longevity with high seed yield, that does not imply that artificial selection cannot do so. Modern annual-grain agriculture has been costly, removing a third of the planet's topsoil in the past half-century [52]. A ∼700% increase in fertilizer use (accompanied by increased use of pesticides) has bolstered productivity and countered the effects of soil loss, but with declining marginal returns in yield [65]. The external costs of crop production in the United States are $5–16 billion per year ($29.44–$95.68 per hectare) [63]; in the UK this figure was estimated at $330/ha [54]. Given this, expanding and further developing sustainable forms of agriculture is paramount.

Perennial grain crops have the potential to help meet this goal by providing ecosystem services in addition to yield. Properly developed, it is expected that such crops may decrease input costs, sequester nutrients, retain and form soil, benefit pollinators, suppress weeds, and sequester carbon dioxide [16, 22, 51, 57]. Due to this, one economic comparison has estimated that profit from perennial systems may equal that of annual systems at only 70–80% their yield [5]. Another study accounting for equipment and input costs determined that a perennial yield of 673 kg/ha/yr for four years would have a similar break even price to spring wheat. [69] Depending on the assumptions used, Pimentel et al. [51] found that perennial wheat could be 48% more to 30% less profitable than annual wheat.

Despite these potential benefits, breeding efforts have been limited, and decades of breeding through existing efforts have yet to establish a variety that produces near this level. [15, 68]

For instance, 25 years of work on an annual-perennial by Suneson, Sharkawy, and Hall [61] produced strains whose first-year yields were comparable to the lowest yielding commercial wheat varieties of the time. Scheinost et al. [58] has developed perennial wheat lines which yield 1600–5800 $^{kg}/_{ha}$, in comparison to the 9000 $^{kg}/_{ha}$ yielded by a popular annual variety.

However, this is not to say that no progress has been made. Intermediate wheatgrass, now commercialized under the name Kernza, has reached a yield point where it is almost profitable to sell it as a specialty group to a set of consumers willing to pay a premium for products of this nature (Lee DeHaan, personal communication). Unfortunately, this niche market is not large enough to drive the widespread plantings necessary to produce many of the hoped-for benefits for society. Higher yield levels are necessary to encourage widespread adoption.

2.2 Why don't we have perennial grains already?

In a sense, we already do have perennial grains: woody perennials such as palm nut and sugarcane living in tropical regions produce some of the highest yields of any plants. Therefore, the real question of interest is why we do not yet have high-yielding herbaceous perennials to compete with the annual crops whose yields dominate the temperate climates. (A separate question of whether it is possible to grow high-yielding woody perennials in temperate regions is not considered here.)

The lack of success in breeding high-yielding herbaceous perennials has led some to propose that such plants may be unable to ever yield at levels equal to or greater than annuals. [60, 68] Van Tassel, DeHaan, and Cox [66] discuss five categories of hypotheses to explain this and consider the plausibility of each. Although not all of these hypotheses, e.g. those relating to genetic factors, can be directly addressed by the theory described here, several can.

The set of hypotheses that I address here are those that consider high-yielding herbaceous perennial grains to be logically or thermodynamically impossible. This suggests a nexus of subhypotheses: (a) Longevity may be energetically expensive, thereby forcing perennials into low-yield states. (b) High yield levels may be offset by low levels of yield during establishment. Therefore, although perennials may be able to out-yield annuals in a given year, annuals will still produce more net yield. (c) Perenniality in herbaceous plants is more expensive than in woody plants such that herbaceous perennials will never out-yield herbaceous annuals.

I will return to these hypotheses later in this thesis. Ultimately, Van Tassel, DeHaan, and Cox [66] conclude that the simplest explanation for the absence of high-yielding perennial

grains is that it is not possible for them to evolve via natural selection. This agrees with my own conclusions.

2.3 The Role of Theory

Given the long time-frames of developing high-yielding herbaceous perennial grains it may take many years and great expense before their feasibility can be determined empirically. However, theoretical ecology can offer valuable insights into whether or not such a plant can exist and may even be able to provide guidance for how it may be bred.

Ecological models generally predict obligate trade-offs between long-lived plants which produce low seed biomass (perennials) and short-lived plants which produce more seed biomass (annuals) [18]. Since the breeding of perennial grains is predicated on the feasibility of developing variations which are both high-yielding *and* long-lived, this is problematic. However, these predictions of trade-offs between longevity and yield may be the result of the way existing models are formulated.

Simple ecological models tend to explore equilibrium states and often preassume plants' life strategies by treating properties such as longevity and yield, and the trade-offs between them, as independent variables to be specified prior to running the model. More complex models have been used, but largely to explore systems governed by natural selection. [23, 64] Plant specific models are an alternative and have been used to explore ideotypes in agriculture, but suffer from large numbers of parameters, and focus on yield optimization through manipulation of species-specific properties. [26]

In light of this, if general questions regarding longevity and yield are to be answered, standard approaches may be insufficient: a new approach is required. This approach must be able to express artificial selection, explore unstable evolutionary states, and capture behavior of plants of a kind that do not yet exist.

How can this be done? By modeling life strategies as emergent properties. Hyperbolically, it would be difficult or impossible to determine that large dinosaurs could exist by synthesizing information about the morphologies and life histories of reptile and other species alive today. But by considering the fundamental biological systems and constraints that give rise to these patterns, it may be possible to show that an animal of such proportions is possible.

In this thesis, I use theory and modeling to quantify trade-offs surrounding yield and longevity, and to predict the kinds of selective regimes that may produce hitherto elusive high-yielding perennial grains.

2.4 Alternate Approaches

But how can such models be formulated? There are three classes of models I will consider before I ultimately settle on the last one: whole-system models, plant specific models, and resource allocation models.

2.4.1 Whole-System Models

Whole-system models, as I term them here, discover optimal life strategies indirectly by modeling couplings between the environment, competitive interactions, and internal dynamics of plants.

The work of Bornhofen, Barot, and Lattaud [6] is an example of such a model. Bornhofen models plants using L-systems: these are simple grammars that describe the branching patterns of stems and roots, along with the location and quantity of seeds produced. A plant's L-system can be used to develop detailed models of light-capture, nutrient acquisition (see Leitner et al. [40] for a specific example of this, along with a good introduction to the use of L-systems in plant architecture modeling), and internal nutrient/carbon demands. Conveniently, rules for combining and mutating L-systems can be defined enabling evolutionary processes. Using this approach, Bornhofen explores the behavior of communities along gradients of stress and disturbance.

Earlier iterations of my work (unpublished) also took a whole-system approach. I modeled competition between pairs of competing plants over multi-year periods with yield determining representative concentrations in the gene pool. I solved the model using genetic algorithms to optimize systems of hundreds of variables representing monthly allocations to roots, leaves, stems, and seeds. In this work, perennials yielded more than annuals across many of the environmental conditions I sampled. Perennials also constructed more resource-gathering tissues than were necessary to capture 100% of nutrients: excess tissue was being made in order to compete effectively. However, these models were difficult to explain and parameterize, and produced predictions that would be difficult to test.

Other such detailed models have been created (see, for instance, 48, 59, 64, 71), but the above two are representative of the approaches used, drawbacks, and the degree of complexity in this class of models. While I discuss this class of models in terms of my own and Bornhofen's work, it is important to bear in mind that the problems identified are general to the approach taken.

(a) The results are difficult to duplicate. Bornhofen did not publish code and, when I inquired about it, told me he considered it too messy to share. This is not unusual, my

own source code is difficult to interpret. Other models, such as `ALLOCATE` [64] were available as source code from the author, but have been lost over time with only mathematical and textual descriptions remaining. Therefore, it is important to be able to capture as many details of a model as possible in the publication relating to it.

(b) Running the models was time consuming. Bornhofen's work required ten hours per simulation on a desktop; this, in turn, reduced the number of runs made such that Bornhofen's results are based on a mere twenty realizations of the model. My work required perhaps five minutes of run-time on a supercomputer, but many runs were needed because the model did not always converge.

(c) Convergence is an issue. All of these models require many runs to smooth the stochasticity of the underlying systems and ensure that optimal solutions have actually been found.

(d) Statistical analysis of the results was necessary. For instance, Bornhofen used PCA to determine that the plants had differentiated into competitors, stress-tolerators, and ruderals (a partitioning suggested by Grime [24]).

(e) The plant strategies that arise from such models are the result of interactions between the way individual plants, the environment, and competitive interactions are modeled. In my earlier work after an optimal allocation strategy had been found, the only way to visualize that strategy was to run it against another plant. As such, the models are most useful for asking the question "What do plants do?" rather than the question "What can plants do?"

(f) It is difficult to trust the results of such models. In scientific computing we do not know ahead of time what the results may be. The model's implementation may be incorrect, but the results may still look reasonable. For example, if an error in a climate model results in slightly different temperatures no one may notice. Ultimately, complex models are difficult to build and, relatedly, it is difficult to find people willing to take the time to understand and verify them.

Issues relating to code publication and correctness have been discussed frequently in top journals (a few examples from *Nature* include [4, 14, 28, 44]) and it is rumored that NSF-funded projects will have to release code in the future. Given the epistemological and scientific difficulties associated with complex models, it seems wise to rule out simpler formulations before resorting to them.

2.4.2 Plant Specific Models

Plant specific approaches try to explain a plant's growth and yield using detailed models of the plant's environment and physiology. In some cases, despite the name I have used here, the models are generic but made specific through suitable parameterizations and choices of

functions. The GECROS model presented by Xinyou and Laar [70] is one such example. The model uses approximately 600 variables to define transpiration, organ growth, resource allocation, resource remobilization, and nutrient uptake, in addition to other processes. Early versions of LPOTCO, a truly plant-specific model of potatoes, utilized approximately 60 variables to model many of the same processes. [38] Aside from the difficulty in parameterizing such models and determining the appropriate functions through which the parameters relate to each other, these models are built to model only a single growing season; thus, they cannot be used determine under what conditions annuals might be favored over perennials and vice versa.

2.4.3 Resource Allocation & Investment Models

The idea behind this class of model is to maximize a plant's reproductive output or some other trait or weighted combination of traits by optimizing over choices the plant can make.

This approach explicitly assumes allocative trade-offs. Grubb [25] claims that the concept of trade-offs is often evoked too loosely, that most trade-offs have organisms which serve as counter-examples to the trade-off, and that some trade-offs are boundaries rather than surfaces so that there are broad state spaces in which simultaneous increases in quantities can be achieved without a trade-off being experienced. While breeders have used similar arguments to counter the claim that simple trade-offs would prevent a high-yielding perennial [15]. Therefore, my models serve as a limiting case: if trade-offs are non-absolute than the modeled plants should be able to yield at higher levels.

Early work on such models focused on discrete-time formulations in which the choice was what fraction of a population should reproduce or germinate in a given year. [9, 11, 12] More recently, optimal control theory has been used to find continuous-time descriptions of resource allocations using an environmental model, a plant model, a definition of the interface between these, and a fitness function—typically reproductive mass—control theory is used to determine how much, at what time, and to what organ a plant should allocate photosynthate given potentially limited resources and growth time. In some cases closed-form analytic solutions can even be found. Approximately sixty-two papers have been published using this technique, primarily by Dan Cohen, Yo Iwasa, and Jan Kozłowski with a number of other authors making separate contributions. This body of work has been dominated by considerations of annuals and single growth seasons. [10, 17, 19, 41, 62, 67, 73]

Only a few works have considered the question of optimal perennial strategies. The most common approach has been to use control theory to find optimal single-seasons strategies and then to string multiple seasons together using dynamic optimization, similar to the

early discrete-time formulations. Mirmirani and Oster [45] was one of the first to use this approach, but their results are inapplicable to herbaceous organisms since they assume that a plant's vegetative components survive winters, though this simplification allows them to consider two interlinked plant models.

Using a model with a vegetative and a storage compartment, Iwasa and Cohen [31] assume that all vegetative tissue is lost over the winter and explicitly considers trade-offs between longevity and yield. However, they limit their analysis to the ratios of initial to final seed mass of the steady state multi-season strategy. Here, I will build on this work by considering absolute yields over a time period including establishment. Furthermore, as will be explained below, I remedy several unrealistic points of the model including (a) lack of metabolic costs and (b) lack of competition.

Pugliese and Kozłowski [55] introduce a separate reproductive compartment and consider cases in which a fraction of the vegetative tissues survive the winter; however, they consider only perennial plants and do not explore the transition between annual and perennial strategies.

Mironchenko and Kozłowski [46] introduce a continuous-time seasonal model with no discrete-time components and demonstrate that it can express annual, perennial, and biennial strategies. The complexity of this model is such that I do not use it here.

2.5 My Approach

In the following, I will use a simple continuous-discrete resource allocation model similar to that presented by Iwasa and Cohen [31]. As I discuss in Equation 4.1 on p. 32, dividing the model into discrete seasons provides considerable simplification over the model by Mironchenko and Kozłowski [46] without sacrificing too much detail. Using control theory to relate important environmental variables to plant physiology may result in models which can be complicated to analyze mathematically, but offers elegant model formulations and is amenable to simple numerical presentations. For this reason, it is preferable to a whole system or plant specific model.

Aside from these technical reasons, this approach fits with a philosophy motivated by the modeling problems discussed above.

The difficulties associated with understanding and parameterizing whole system and plant specific models evoke the following point...

> *The danger in creating fully detailed models of complex systems is ending up with two things you don't understand — the system you started with, and your model*

of it. -Philip England and Chris Paola [49]

Modeling life history in terms of investment strategies which can be expressed through a limited number of simple equations ensures that the model's parts are understandable and, even though complex math may be needed to solve the model, the results are easily understood and compared with intuition.

The danger in adopting a simple model is that inevitably, someone will identify what they consider to be important variables or processes that have been omitted. The approach used here will certainly have some omissions. A second philosophical point considers this...

All models are wrong, but some are useful. -George E. P. Box [7]

I view my models as representing limiting cases of more complex systems. As such, I argue that they plausibly capture trends which more complex systems would have to include. If this is so, then the addition of greater complexity may result in minor changes in individual results and the addition of caveats and exceptions, but none of this would undermine the existence of the trends I identify.

A final point is that...

A theory should contain only those things which we can, in principle,measure.

Accordingly, wherever possible, I try to identify possible sources and values for the variables used in my models.

Chapter 3

The Model

The goal of a plant is to make more of itself. To do this, a plant builds *productive tissues* which acquire energy and nutrients, such as leaves and roots. A plant may also build *competitive tissues* such as stems, thorns, or chemical defenses. Excess energy and nutrients which are not allocated to productive and competitive tissues can be allocated to *perennating storage tissue* or *reproductive tissues*.

3.1 Finding an optimal multi-season strategy

Let us assume that perennating storage tissues and reproductive tissues are both sinks which do not act to enhance production or competition during a growing season, and which only become valuable once a new growing season has begun (perennating storage) or a new plant has sprouted (reproductive tissue in the form of seeds). In this case, assuming the two tissue types have equivalent construction costs, we can mathematically treat the two as a common storage sink during the course of a growing season and determine the optimal ratio of storage to seeds at the end of a season.

Specifically, let the mass of the combined storage pool be represented by S and the mass allocated to reproduction as R. Then the amount of storage dedicated to perennation is $S - R$. If some fraction γ of the perennating mass is lost between growing seasons, then a plant which pursues a perennial strategy will begin the new growing season with storage mass $\gamma[S-R]$. Let us assume there exists some function $\psi_T(S)$ which maps the initial storage or seed mass of a plant to its optimal storage mass after a growing season of duration T. Given this, we can describe a plant's life cycle as follows.

A plant begins life with some storage mass S_0 (the mass of the seed it sprouts from) and

Symbol	Description	Units
n	nth year of a plant's life	$\in [0, \infty)$
R	Amount of storage allocated to seeds	g
S	Final storage size after growing season	g
S_0	Initial storage size	g
T	Duration of a growing season	days
V_n	Reproductive value of years n–∞	g
γ	Winter survival fraction	$\in [0, 1]$
σ	Discount rate	$\in [0, 1]$
$\psi_T(S)$	Optimal storage size given S_0 after a season of length T	g

Table 3.1: Variables used in the multi-season model

ends its first growing season with a storage mass $\psi_T(S_0)$. Of this final storage mass, we retroactively declare that some mass R was actually seeds. The remainder, $S - R$ overwinters as described above and the process begins again. In the limiting case, no productive or competitive tissues survive the winter and growth must begin anew from whatever storage the plant did not allocate to reproduction.

The total "reproductive value" of a plant is the sum of the R values for each growing season it lives. But, since the future is uncertain, a rational plant will value future reproduction less than present reproduction. The simplest way to account for this is to assume that a plant values each subsequent year a fraction σ less than the preceding year. σ can also be viewed as an economic discount factor, since a farmer will, in most cases, value near-term gains over riskier long-term gains.

Mathematically, the ideas above can be captured by a Bellman-Ford equation:

$$V_n(S) = \max_{0 \le R \le S} \left(R + \sigma V_{n+1} \left(\psi_T \left(\gamma \left[S - R \right] \right) \right) \right) \tag{3.1}$$

where the variables are as described above and in Table 3.1. The equation may be solved either by recursion to a given depth after which reproduction has no value (say, $V_{n>8} = 0$) or until a steady state is achieved ($V_n = V_{n+1}$).

I solve this equation using dynamic programming in `C++` as follows:

Implementation 1: Implementation of the Multi-season Model

```
1 void OptimalPath(
2   bool        replant, //Replant annuals
3   double      sigma,   //Discount rate
4   double      gamma,   //Over-winter loss
5   const Svals &S0s,  //Initial storage masses (along with Sfs this is ψ_T)
```

```
  Svals       &Sfs,  //Optimal final storage masses (ψ_T)
  int         n,     //Number of years over which to optimize
  values_t    &values, //Matrix of reproductive values for each year
  choices_t   &choices //Matrix of optimal allocation choice for each year
){
  //'values' and 'choices' are two-dimensional matrices which cache
  //the reproductive value and optimal choices of subsequent years so
  //that they can be quickly looked up, rather than recalculated, in
  //the years which precede them. This turns an exponential
  //calculation O(n**len(Sfs)) into a O(n*len(Sfs)) problem.

  //If the initial storage is zero force the final storage to also be
  //zero. It may be slightly larger due to floating-point math.
  Sfs[0] = 0;

  //The final storage values represent the spectrum of possible
  //choices of storage to retain for a future year. We can
  //precalculate which cell on the horizontal (storage mass) axis of
  //the values matrix to look up for each possibility. Sf[s] is an
  //over-winter allocation, gamma*Sf[s] is the amount of that
  //allocation which survives the winter, FindLargest() is a function
  //which determines which initial storage mass is closest (but not
  //larger than) the amount which survived the winter. The final
  //storage mass associated with this is used in the Bellman equation.
  std::vector<int> PsiGammaS0(Sfs.size(),0);
  for(int s=0;s<Sfs.size();s++)
    PsiGammaS0[s] = FindLargestLessThanEqualNeedleIdx(S0s, gamma*Sfs[s]);

  //Work backwards in time from some future date to the present
  //determining the optimal values as we go.
  for(int t=n-1;t>=0;t--)
  for(int s=0;s<Sfs.size();s++){ //Consider each final storage size
    //These two variables define the optimal choice of storage mass to
    //save for the next season and the value of that choice. They are
    //initialized to dummy values that will be overwritten on the
    //first iteration of the loop.
    int bestchoice = -1;
    double bestval = -1;
    //All final storage sizes less than or equal to the current one
```

```
45      //are candidates of storage that can be saved until the next
46      //season. Consider them all unless replanting is activated, in
47      //which case force a perennial strategy
48      if(!replant){
49        for(int skeep=0;skeep<=s;skeep++){
50          //Determine the future value of the allocation choice. If this
51          //is the final time, there is no future value at all; otherwise,
52          //we fetch the cached future value.
53          double val = (t==n-1) ? 0 : sigma*values[t+1][PsiGammaS0[skeep]];
54          //Add to the future value the present value.
55          val += (Sfs[s]-Sfs[skeep]);
56          //If this is the best choice we've seen so far, make a note of it.
57          if(val>bestval){
58            bestval    = val;
59            bestchoice = skeep;
60          }
61        }
62      } else {
63        bestchoice = 0;
64        bestval    = (t == n-1) ? Sfs[s] : Sfs[s]+sigma*values[t+1][s];
65      }
66
67      //Cache the best choice and value for this time and initial
68      //storage value
69      values [t][s] = bestval;
70      choices[t][s] = bestchoice;
71    }
72  }
```

Implementation 1: Implementation of the Multi-season Model

The formulation so far is a simple model of a trade-off between current and future gains given an environment with losses and discounting. If there were a simple way to relate the initial and final storage sizes across a growing season to each other, we could analyze this model alone in search for answers. However, in general, the relationship between these two may not be simple and will itself be a function of environmental variables.

How then should $\psi_T(\cdot)$ be defined?

3.2 Finding an optimal growth season strategy

In the sections to come, I will develop several single season models with which to define $\psi_T(\cdot)$. The first will be a limiting case in which there is no metabolism or competition. The second model introduces metabolism and the third introduces competition.

In this initial iteration of the model, the plant is assumed to consist of only two types of tissue: productive tissue P, which encompasses both leaves and fine roots, and storage tissue S, which includes all perennating and reproductive tissue. The plant sprouts from a single seed with storage mass S_0 and productive mass P_0; P_0 is generally quite small. I do not yet consider metabolism and competition. Since I am consider herbaceous plants, at the end of a growing season, all of the productive tissue will be lost.

The productive tissue P produces new structural material according to a function $g\big(P(t)\big)$. This material may be used to build either additional storage tissue S or additional productive tissue P. However, at the end of a growing season of duration T, the goal of the plant is to maximize its storage $S(T)$; this will be divided into perennating and reproductive tissues, as explained below.

But how can $S(T)$ be maximized? An early lesson in calculus is to determine the maximum of a function by considering how the function changes with respect to a variable. There is a branch of mathematics called "optimal control theory" which extends this paradigm by considering how a system of equations changes with respect to a function and provides tools for finding this function. Perrin and Sibly [50] discusses these techniques in the context of ecology while Kamien and Schwartz [34] is an excellent resource for the techniques themselves.

Therefore, to determine what gets allocated where and when, I cast the model as a control problem. New photosynthate is apportioned between P and S by a control $0 \leq u(t) \leq 1$ such that new productive tissue is added at a rate $u(t)g\big(P(t)\big)$ and new storage tissue is added at a rate $\big(1-u(t)\big)g\big(P(t)\big)$. If the plant allocates to P, then the values of $g\big(P(t)\big)$ become larger, which aids in further growth;

Additionally, resources can be withdrawn from storage in order to construct productive tissue. This transfer occurs at a rate $w(t)aP$, where a scales the transfer rate and $w(t)$ is a control such that $0 \leq w(t) \leq 1$. This internal reallocation is necessary for a seed to be able to utilize its stored energy or for a perennial to be able to save resources from one growing season to the next.

It is possible to use only a single control here by transferring resources out of storage at a rate $u(t)aP$ instead of $w(t)aP$. Using one variable is physically sensible since it would not be logical to allocate new photosynthate to storage while simultaneously reallocating

storage to production; it could also be mathematically convenient since the system will reach the same final state but fewer equations would be necessary. However, the behavior of the control would be more complex. With two controls, both controls are bang-bang while with one control $u(t)$ must take on an intermediate value (singular arc) in order to ensure the constraint $S \geq 0$ is satisfied. This behavior could be suppressed by multiplying the transfer rate $u(t)aP$ by a sigmoid function so that the transfer is expressed by $u(t)aP\frac{1}{1+e^{-20(x-0.9)}}$. The effect of this is that full transfer from storage is possible until the storage is very nearly exhausted, at which point no transfer is possible. This ensures that the constraint $S \geq 0$ can be satisfied without the need for a singular arc, but increases the complexity of the equations. Another alternative is to express the transfer rate as $u(t)aPS$, so that as $S \to 0$ so to does the transfer, thereby ensuring $S \geq 0$; however, this materially affects the behavior, final state, and physical description of the system. For these reasons, two controls are used.

In contrast to the current model, Iwasa and Cohen [31] initially apportion all new production to storage and reallocate storage to production according to a control $0 \leq u(t) \leq 1$ at a rate $0 \leq u(t)(aP(t) + b) \leq (aP(t) + b)$. Their model assumes that $P_0 = 0$; therefore, b is required if any growth is to occur, but becomes inconsequential as P increases. One way of interpreting this model formulation is that a constant amount of growth is always possible, regardless of the size of the plant. A convenient aspect of this modeling choice versus my own is that under unfavorable conditions a plant will not grow at all; whereas, in my model, the plant will very slightly increase the size of its storage due to the presence of $P_0 \neq 0$. The inclusion of any amount of tissue loss would fix this. In practice, this does not affect my conclusions.

Since, as discussed above, the behavior of the plant does not depend on S after the plant has established itself for the season, some portion of the storage mass can be retroactively declared to be seeds at the end of the growing season. This mathematical convenience eliminates the need for a separate state variable for reproduction. In any case, maximizing end-season storage also maximizes the fitness of the plant in this scenario since more storage means either faster regrowth in a subsequent growing season or more seeds at the end of the current season.

Note that this model explicitly represents trade-offs between vegetative, perennating, and reproductive allocations. Some authors (e.g.) have argued in favor of high-yielding perennials by arguing that trade-offs between these structures may not be strict. Insofar as this view is correct, the model presented here provides a more stringent test and, therefore, represents a lower bound of what yield is possible.

Modeling details are given in §B.1 on p. 46 and the variables used and their units are shown

Symbol	Description	Unit
t	Time in the growing season	days
$P(t)$	Productive tissue mass	g
$S(t)$	Storage tissue mass	g
$u(t)$	Control for new resource allocation	$\in [0, 1]$
$w(t)$	Control for storage transfer	$\in [0, 1]$
T	Growing season duration	days
a	Storage transfer rate	$\frac{0.2\,\mathrm{g}}{\mathrm{g}\cdot\mathrm{day}}$
$g(P)$	Production rate	g/day
P_0	Initial mass of productive tissue	g
S_0	Initial mass of storage tissue	g
$g_{\max}$	Maximum production rate	g/day
K_P	Half-saturation constant of production	g

Table 3.2: Variables used in the simple single-season model

in Table 3.2 on p. 16. Mathematically, the system is described as follows.

$$\dot{P} = g(P)u(t) + w(t)aP \tag{3.2}$$

$$\dot{S} = g(P)\big(1 - u(t)\big) - w(t)aP \tag{3.3}$$

$$P(0) = P_0 \tag{3.4}$$

$$S(0) = S_0 - P_0 \tag{3.5}$$

$$0 \leq u(t) \leq 1 \tag{3.6}$$

$$0 \leq w(t) \leq 1 \tag{3.7}$$

$$S(t) \geq 0 \tag{3.8}$$

$$P(t) \geq 0 \tag{3.9}$$

$$S(T) \to \text{maximum} \tag{3.10}$$

There are several ways to define $g(P)$. Iwasa and Cohen [31] use a function suggested by Cohen [67]

$$g(P) = \frac{fP}{1 + hP} \tag{3.11}$$

where f is the maximum net production rate (the maximum relative growth rate) and h is a self-limiting coefficient. Mathematical manipulation of Equation 3.11 reveals the familiar Monod or Michaelis–Menten equation:

$$g(P) = \frac{fP}{1 + hP} = \frac{f}{h}\frac{P}{1/h + P} = g_{\max}\frac{P}{K_P + P} \tag{3.12}$$

where $g_{\max}$ is the maximum rate of production and K_P is the half-saturation constant: the point at which $g(P)/g_{\max} = 0.5$. Note that the non-linearity of this production function means

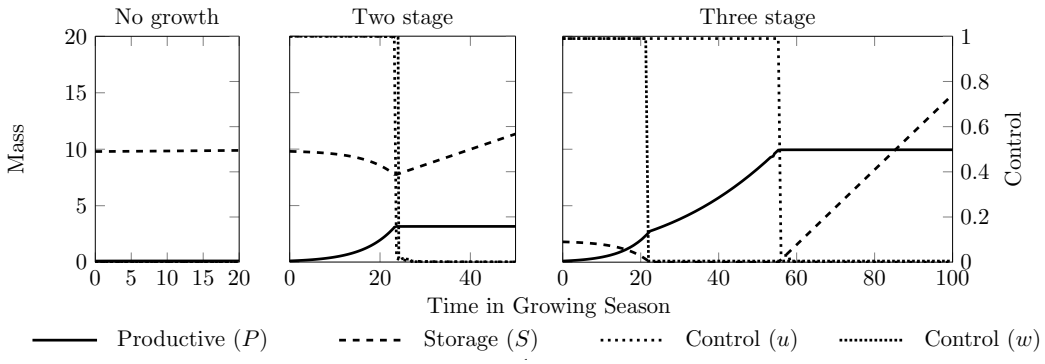

Figure 3.1: Different optimal growing season strategies. The strategies are characterized by how the plant's storage mass changes. In the "No growth" scenario it does not change. In the "Two Stage" scenario, storage decreases, but does not empty, and then regenerates. In the "Three Stage" scenario the storage empties entirely and the plant enters a period of purely vegetative growth, and then regenerates.

that general closed-form solutions to the governing system of equations cannot be found. Iwasa and Cohen [31] use $f = h = 0.05$ for all of their models. Translated into the terms of Equation 3.12, this is $g_{\max} = 1, K_P = 20$. I adopt this value for my own simulations.

Lavigne [39] and Meer [43] use a different production function

$$g(P) = aP^b \tag{3.13}$$

for $b \geq 0$; however, while analytically attractive, this function has the disadvantage of being non-saturating: self-shading and limitation never reaches the point where production levels off. I do not considering this function further here.

While optimal control theory can be used in a subset of cases to find analytical solutions to problems, the mathematics is often complex. Since a discrete-continuous formulation is used here, it is unclear that the generality of an analytical solution to the single-season model would provide much benefit to analyzing the system as whole. Therefore, I use JModelica [1] to find numerical solutions to the control problems.

Three general optimal growing season strategies are possible, as shown in Figure 3.1. In the "No Growth" scenario, any vegetative tissue that could be converted from the storage tissue will never pay for itself; therefore, no storage tissue is converted. Another way of thinking about this is that there are some environments in which life is not possible: the optimal strategy for a seed in those environments is not to sprout, perhaps in hopes that the environment will improve. In the "Two Stage" scenario, the initial mass of storage is large enough and the growing season short enough that there is never a time when the storage is entirely consumed and goes to zero. In the "Three Stage" scenario, the initial mass of

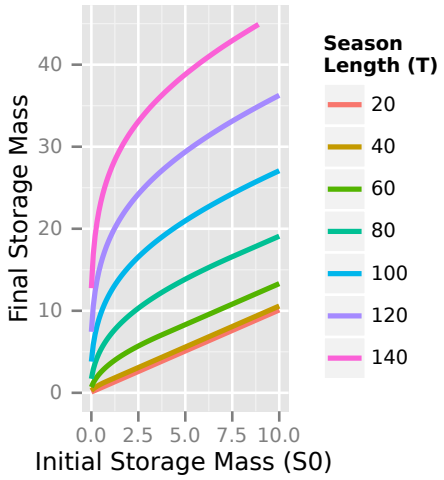

Figure 3.2: A graph of the function $\psi_T(\cdot)$ for various parameters.

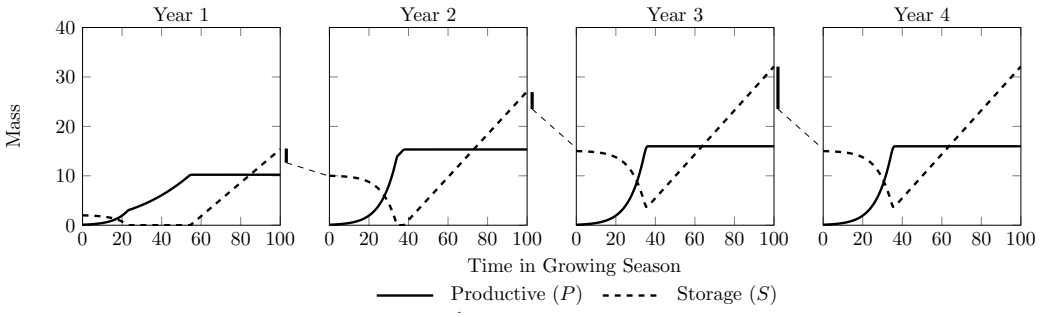

Figure 3.3: An optimal multi-season strategy for a plant whose initial seed mass is 2. Note the rapid convergence to a steady-state solution by the end of the third year. Also note that the highest potential yield (assuming no winter-loss) of the first year is 15 units, whereas, by the third year, yields of 25 units are possible.

storage is small enough and the growing season long enough that there is an interval of purely vegetative growth.

Collectively the foregoing can be used to define the missing function $\psi_T(\cdot)$ required for the multi-season model.

3.3 Combining the Models

§3.1 on p. 10 describes a model for optimal multi-season investment given a function $\psi_T(S)$ which gives the optimal end-season storage for a plant of initial storage S_0 over a growing

season of duration T. §3.2 on p. 14 describes a model which can be used to define $\psi_T(S)$. Combining the two models permits the exploration of multi-season strategies.

Figure 3.3 on p. 18 depicts one such strategy. From an initial seed mass of 2 units, the plant grows to have a storage mass of 15 units. Of these, 2.5 units of storage are devoted to reproduction and 2.5 are lost to over-wintering. The remaining 10 units of storage are used to initiate growth in the second year. At the end of the second year, the plant has 25 units of storage of which 10 are either used for reproduction or lost leaving the plant with 15 units of storage. This leads the plant to a steady-state: year four, and all subsequent years, employs the same strategy as year three.

3.4 Analysis

For an organism to be able to execute any of the model's strategies, it must be able to mimic the behavior of the controls u, w. Figure 3.1 on p. 17 suggests that this should not be challenging since both of the controls are bang-bang. The w control transfers resources from storage into production tissue until either the storage is exhausted or storage building begins. Similarly, the u control transfers all new photosynthate into production tissue until storage building begins. Therefore, the only information a plant needs to know in order to execute the optimal strategy is when to make these switches. This requires sensing storage mass and either an internal timer or a seasonal cue.

To characterize the possible outcomes of the model, I perform a parameter sweep of the model's free variables, which are (a) the initial seed mass S_0, (b) the growing season length T, (c) the proportion of storage materials which last until the next growing season γ, and (d) the probability of survival σ. The code to perform the sweep is detailed in §B.4.

Four strategies are shown in the parameter sweep depicted in Figure 3.4 on p. 20. The "Perennial" strategy arises when a plant's best strategy is to grow back year after year, sacrificing immediate gains in reproductive value for smaller, recurring gains. The "No Growth" strategy dominates when growing seasons are too short and initial seed sizes too small for a plant to get any return on investment from making productive tissue. The "Annual" strategy represents a situation in which a plant allocates all of its resources to seed at the end of its first growing season and none of these seeds survive. This is the most common outcome for most annuals in nature. The "Replanted Annual" strategy represents a situation in which a plant allocates all of its resources to seed at the end of its first growing season, and one seed is guaranteed to survive. This is the agricultural outcome: every plant that is harvested is replanted.

With this in mind, we can now pose and answer the following questions.

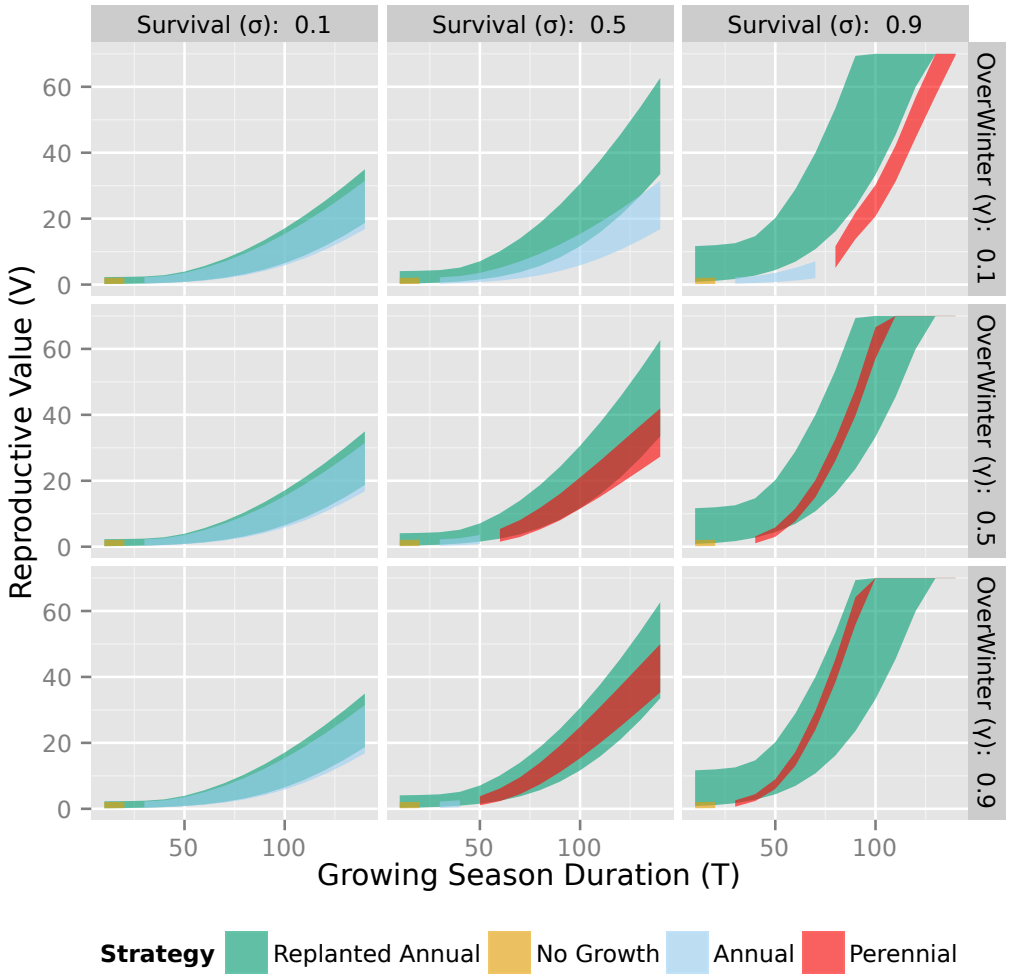

Figure 3.4: A parameter sweep of the free variables of the model for $n = 8$. The spread indicates reproductive values for all initial seed masses ≤ 2. In the most productive environments, the reproductive values are higher than can be shown in the figure. This figure is discussed on p. 19.

What strategies dominate in the long-term if no replanting takes place? To answer this question, we set $n = 8$ in the multi-season model and perform a parameter sweep. The results are shown in Figure 3.4 on p. 20 if you ignore the "Replanted Annuals" data. In truly unfavorable environments characterized by short or extremely short growing seasons the No Growth strategy dominates. In environments made unfavorable by low survival rates or high over-winter loss, annuals dominate. Perennials dominate favorable environments.

Do perennial strategies out-yield annual strategies if annuals are replanted? If we view the

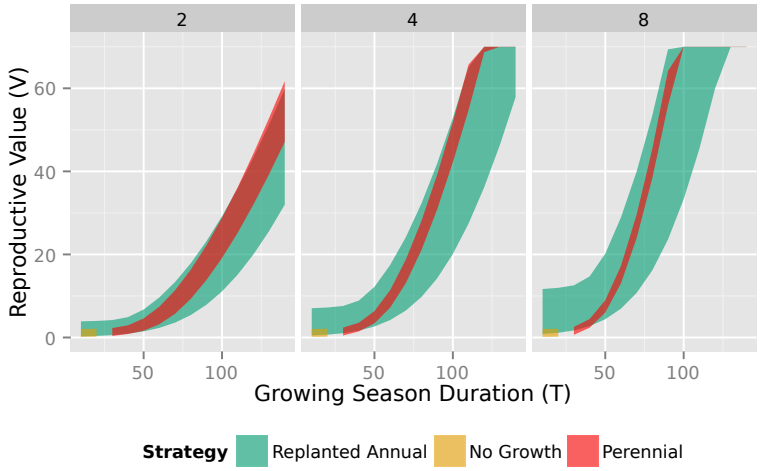

Figure 3.5: The effect of planning horizons on value. The results are shown for an environment with low discounting ($\sigma = 0.9$). Each of the panels represents a different value of n. The rightmost panel is the same as the bottom right of §3.3 on p. 19.

multi-season model in terms of site occupation, then, if the model favors an annual strategy, the annual's site is left unoccupied for every year but the first. In an agricultural setting site occupation is both enforced and guaranteed so Equation 3.1 on p. 11 no longer applies; instead, the following equation must be explored:

$$V_n(S_0) = \psi_T(S_0) + \sigma V_{n+1}(S_0) \tag{3.14}$$

Each year the full reproductive output of a plant is collected. In subsequent years the same plant sprouts from a seed of the same size and its reproductive output is discounted appropriately. In Implementation 1 on p. 11 setting the variable `replant` to true invokes this behavior.

The result of invoking this behavior is shown in Figure 3.4 on p. 20 under the heading "Replanted Annual". The salient point is that for favorable environments in which annuals are replanted each year, the replanted annuals and perennials produce similar yields, differentiated only by the initial seed size. If perennials sprout from larger seeds than annuals, the perennials' yield may surpass the annuals'. Alternatively, if perennials have access to a longer growing season than annuals, this model projects that the perennials may greatly out yield the annuals. To see this, consider a horizontal cross-section of any of the subgraphs of Figure 3.4 on p. 20: for the most favourable environments a difference of a couple of weeks' growing time is sufficient to offset yield disparities.

How does the number of growing seasons affect this? For environments with high discounting the yield of later years does not make much of an impact on the total value of a plant. Therefore, I approach this question by considering only environments with low discounting ($\sigma = 0.9$) for varying values of n, as shown in Figure 3.5 on p. 21. Across all lengths of planning horizon, the perennials and annuals have similar yields. However, if a short planning horizon ($n = 2$) is used, then potential yields will be lower than if a longer horizon could be used.

Note that the planning horizon, as well as the discount rate, is not just a property of biology, but also an agricultural consideration. The upshot of this is that in a high-risk agricultural setting which demands immediate returns (high discounting), annuals are likely to be the better choice. While perennials can match annual yields in this model, they do so in environments where long planning horizons and relatively low discounting can be accommodated. Practically speaking, crop insurance programs may play an important rôle in creating such an environment.

3.5 Incorporating Respiration and Tissue Loss

The foregoing model of single season growth does not account for respiratory costs and tissue loss (say, to herbivory). In their work, Iwasa and Cohen [31] claim that all of this can be accounted for by Equation 3.11 on p. 16; however, even though that equation approaches an asymptotic limit, unlimited net growth is still possible. The explicit inclusion of metabolic costs and tissue loss combats this and opens the possibility of exploring a wider range of environmental conditions. Additionally, it provides a trivial means of dealing with the mathematical issue of storage increasing slightly under no growth conditions due to $P_0 > 0$.

To incorporate these factors, the foregoing single-season growth model is modified to the following system; variables are defined in Table 3.3 on p. 23 and modeling details are given in §B.2 on p. 47.

$$\dot{P} = g(S,P)u(t) + aPw(t) - l_P P \tag{3.15}$$

$$\dot{S} = g(S,P)\big(1 - u(t)\big) - aPw(t) \tag{3.16}$$

$$g(S,P) = g(P) - \mu_s S - \mu_p P \tag{3.17}$$

$$P(0) = P_0 \tag{3.18}$$

$$S(0) = S_0 - P_0 \tag{3.19}$$

$$0 \leq u(t) \leq 1 \tag{3.20}$$

$$0 \leq w(t) \leq 1 \tag{3.21}$$

Symbol	Description	Unit
t	Time in the growing season	days
$P(t)$	Productive tissue mass	g
$S(t)$	Storage tissue mass	g
$u(t)$	Control for new resource allocation	$\in [0, 1]$
$w(t)$	Control for storage transfer	$\in [0, 1]$
T	Growing season duration	days
a	Storage transfer rate	$\frac{0.2\,\mathrm{g}}{\mathrm{g \cdot day}}$
$g(P)$	Production rate	$\mathrm{g/day}$
P_0	Initial mass of productive tissue	g
S_0	Initial mass of storage tissue	g
μ_s	Respiratory cost of storage tissue	$\frac{\mathrm{g}}{\mathrm{g \cdot day}}$
μ_p	Respiratory cost of productive tissue	$\frac{\mathrm{g}}{\mathrm{g \cdot day}}$
l_p	Loss rate of productive tissue	$\frac{\mathrm{g}}{\mathrm{g \cdot day}}$
$g_{\max}$	Maximum production rate	$\mathrm{g/day}$
K_P	Half-saturation constant of production	g

Table 3.3: List of variables used in the simple model when respiration and tissue loss are included.

$$S(t) \geq 0 \tag{3.22}$$

$$P(t) \geq 0 \tag{3.23}$$

$$S(T) \to \text{maximum} \tag{3.24}$$

The metabolic rates of the production and storage tissues (μ_p and μ_s, respectively) in Equation 3.17 are modeled as being linear in the mass of those tissues. This assumption is supported by Reich et al. [56], who showed isometric scaling in plants from 0.1–10,000 g using data from 500 laboratory and field-grown plants from 43 species. Enquist et al. [21] support the conclusion that seedlings follow isometric scaling, but claim a three-quarter scaling relationship (e.g. $\mu_p^{3/4}$) for plants larger than 1,000 g; Reich et al. dispute this. More recently, Mori et al. [47] have measured the whole-body respiration of 271 plants and claim that the scaling relationship varies continuous, being isometric for plants <1 g and converging to $^3/_4$ for plants ≥100 g. In a case study, Hui and Jackson [27] demonstrate the statistical difficulty of differentiating between competing scaling hypotheses. Since all parties seem agreed that isometric scaling is appropriate for low-mass plants, I use isometric scaling here.

Productive tissue loss l_p is introduced to account for possible herbivory or disease during the growing season.

Representative strategies for long growing seasons are shown in Figure 3.6 on p. 24. To separate the effects of each of the new variables that have been introduced to the model

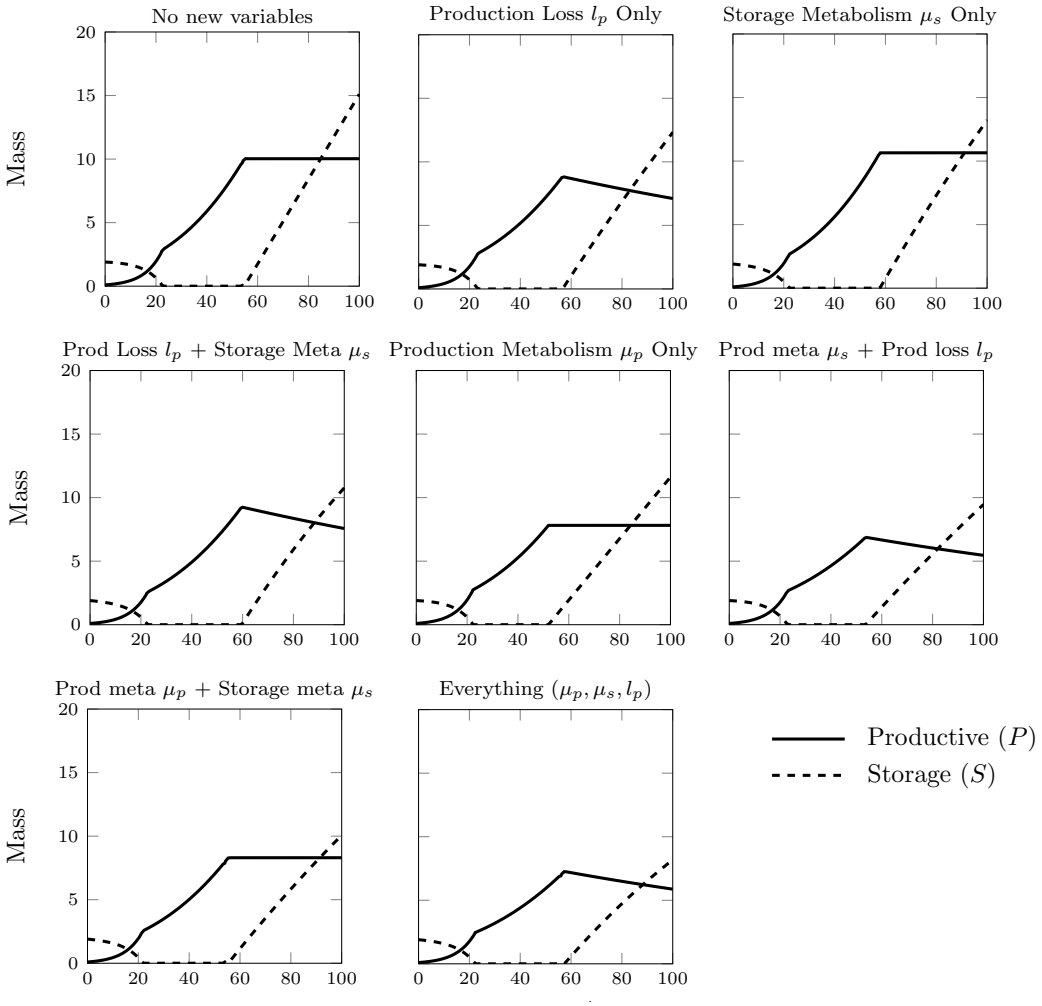

Figure 3.6: Representative strategies for plants in growing seasons of length $T = 100$ for the model with metabolism. The horizontal axis is time within the growing season. The upper left graph, with no new variables included, is the same as is shown in Figure 3.1 on p. 17. To simplify the presentation, the controls are not shown. Metabolic and tissue loss values are set to either 0 or 0.005, depending on the scenario.

(μ_p, μ_s, l_p), each combination of inclusions is tested using a value of 0.005. For comparison, the case in which no new variables are included is also shown; this is the same case as depicted in Figure 3.1 on p. 17.

The incorporation of productive tissue loss results in a longer growth phase for the plant before it ultimately ignores these losses in order to allocate all of its new resources to storage. Including storage metabolism causes the plant to produce more productive tissue versus the no-metabolism scenario to offset the costs. Including production metabolism reduces the

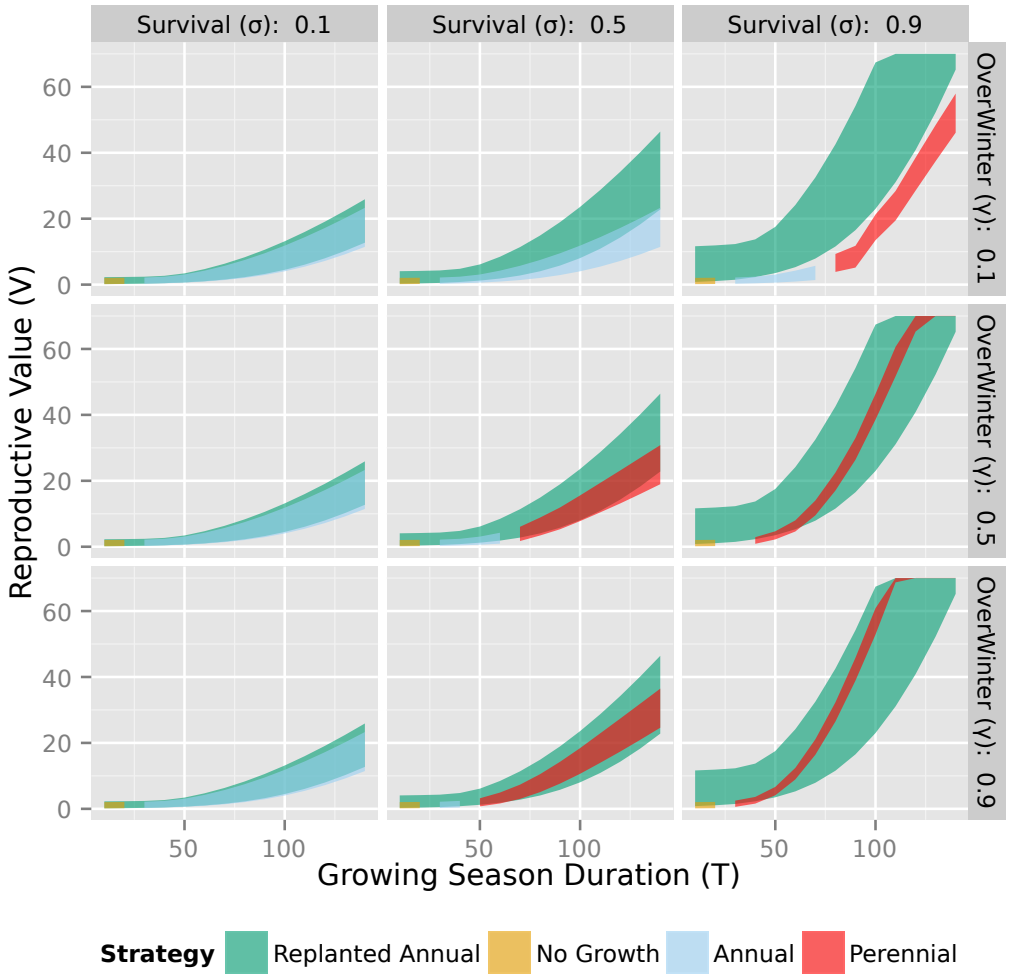

Figure 3.7: A parameter sweep with metabolic costs included for $n = 8$. The spread indicates reproductive values for all initial seed masses ≤ 2. In some cases perennial yields are too high to be shown in the figure. This figure should be compared against Figure 3.4 on p. 20: note that there are only minor differences between the two indicating that metabolism does not affect the result very much.

mass of all of the plant's components.

It is reasonable to assume that tissue loss is negligible ($l_p = 0$); in an agricultural setting plants are protected against this. Similarly, the metabolic cost of storage must be low to negligible ($\mu_s = 0$) or it would not be worthwhile for plants to have storage-like structures.

In contrast, the metabolic costs of production cannot be ignored, though they are low.

For instance, Poorter [53] found that leaves of young vegetative plants meet their construction costs within 1.4–3.6 days, after respiratory costs have been subtracted. Using a now-standard two-part model, McCree [42] found that daily respiration in white clover was equivalent to 25% of daily photosynthesis plus 1.5% the mass of the living tissue. The daily photosynthesis component of this figure can be assumed to be incorporated into the $g(P)$ equation already whereas, in the case of McCree, μ_p would be 0.0015. Amthor [3] surveys a number of works finding maintenance respiration values that range from 0.0002–0.0085 $\frac{\text{g CO}_2}{\text{g·hr}}$. Thus, the value of 0.005 $\frac{\text{g}}{\text{g·hr}}$ used above is reasonable.

Using this value, I perform another parameter sweep over the multi-season model where the single-season metabolic model is used to generate the $\psi_T(\cdot)$ mapping. The results are shown in Figure 3.7. The most important point of this figure is that it differs only marginally from Figure 3.4 on p. 20; therefore, the inclusion of metabolic costs does not significantly change the behavior of the model.

3.6 Competitive Tissue

The foregoing models concern an individual which does not compete with any others. If the foregoing models are viewed as representing cohorts, then the the plants within the cohort do not compete with each other. This results in higher yields and different plant phenology and morphology than would be expected in a natural system.

However, this is not altogether bad. The scenario of interest is an agricultural system in which crops have been bred or positioned to decrease competition. Indeed, annual, domesticated maize crops exhibit many adaptations such as decreased tassel size, increased leaf angle, and smaller leaf sizes versus wild and older variants which decrease inter-plant competition.[20]

One way to account for competition in the model would be to interlink many of the single- and multi-season models to represent different plants and then search for equilibria in this space. However, the resulting model would be quite complex and its optimization challenging. In order to maintain the simplicity of the existing model while still accounting for the effects of competition, I introduce "competitive tissue". This tissue constrains the growth of productive tissues without offering any productive benefits itself. In a highly competitive environment a significant amount of competitive tissue will be required whereas no competitive tissue is necessary to grow in an environment without competition.

Stem tissue is the most obvious form of competitive tissue. In the case of trees, a tall trunk is necessary for the tree's growth while a short trunk dooms a tree to live in shade. Therefore, it is competitively favorable for a tree to increase allocation to its trunk before

it invests heavily in developing a canopy. Thorns are another form of competitive tissue: having too few of them invites herbivory; therefore, the growth of leaves can be viewed as being predicated on the prior growth of defenses. Similarly, chemical defenses can be viewed as a competitive tissue. Leaves may also serve as competitive tissue if they are larger or more numerous solely to shade out competitors.

In the following, I will assume that the plant has low productive tissue loss ($l_p = 0$) and that the metabolic costs of competitive and storage tissues are low ($\mu_c = 0$ and $\mu_s = 0$). However, productive tissues will be assumed to have some metabolic costs ($\mu_p = 0.005$).

Given this, the model with competitive tissue is as follows (see Table 3.4 on p. 28 for variable definitions and units, and §B.3 on p. 47 for modeling details):

$$\dot{P} = \big(g(C,S,P) + aP\big)\, u'(t) \tag{3.25}$$

$$\dot{C} = \big(g(C,S,P) + aC\big)\, w(t) \tag{3.26}$$

$$\dot{S} = g(C,P)\big(1 - u'(t) - w(t)\big) - u'(t)aP - w(t)aC \tag{3.27}$$

$$u'(t) = u(t)\left(1 - \frac{P}{\alpha C}\right) \tag{3.28}$$

$$g(C,P) = g(P)\left(1 - \frac{P}{\beta C}\right) - \mu_p P \tag{3.29}$$

$$P(0) = P_0 \tag{3.30}$$

$$C(0) = C_0 \tag{3.31}$$

$$S(0) = S_0 - P_0 - C_0 \tag{3.32}$$

$$0 \le u(t) \le 1 \tag{3.33}$$

$$0 \le w(t) \le 1 \tag{3.34}$$

$$0 \le u(t) + w(t) \le 1 \tag{3.35}$$

$$S(t) \ge 0 \tag{3.36}$$

$$P(t) \ge 0 \tag{3.37}$$

$$C(t) \ge 0 \tag{3.38}$$

$$S(T) \to \text{maximum} \tag{3.39}$$

The model is similar to those presented above, but incorporates a new state variable C which denotes the mass of competitive tissue. Here I use only two controls. u controls allocation to productive tissues while w controls allocation to competitive tissues. Both controls can tap into the initial storage mass of a seed. Previously this latter ability was delegated to a separate control; however, eliminating it here results in a simpler formulation without altering the results.

Symbol	Description	Unit
t	Time in the growing season	days
$P(t)$	Productive tissue mass	g
$S(t)$	Storage tissue mass	g
$C(t)$	Competitive tissue mass	g
$u(t)$	Control for productive tissue allocation	$\in [0,1]$
$u'(t)$	Competition-modified control	$\in [0,1]$
$w(t)$	Control for competitive tissue allocation	$\in [0,1]$
T	Growing season duration	days
a	Storage transfer rate	$\frac{0.2\,\mathrm{g}}{\mathrm{g}\cdot\mathrm{day}}$
$g(P)$	Production rate	g/day
P_0	Initial mass of productive tissue	g
S_0	Initial mass of storage tissue	g
C_0	Initial mass of competitive tissue	g
μ_p	Respiratory cost of productive tissue	$\frac{\mathrm{g}}{\mathrm{g}\cdot\mathrm{day}}$
α	Competition coefficient	$\in (0,\infty)$
β	Competition coefficient	$\in (0,\infty)$
$g_{\max}$	Maximum production rate	g/day
K_P	Half-saturation constant of production	g

Table 3.4: List of variables used in the simple model when respiration and tissue loss are included

The effect of the competitive tissue is incorporated in two ways. (a) The growth of the plant's productive tissue is modified such that it is limited by the mass of the competitive tissue via the term $\left(1-\frac{P}{\alpha C}\right)$ in Equation 3.28. This is akin to saying that the number of leaves a tree has is limited by the number of branches it has. (b) The plant's production function $g(P)$ is modified so that resource acquisition is conditioned on the competitive tissue via the term $\left(1-\frac{P}{\beta C}\right)$ in Equation 3.29. This is akin to saying that a tree's access to light is limited by the height of its trunk.

The variables α and β are competition coefficients; they determine what returns on investment an individual receives from competitive tissue. High values of α and β mean that a little competitive tissue pays a large dividend. If α and β are infinite, the model degenerates to those forms studied previously. If α and β are low, then significant amounts of competitive tissue are necessary for the plant to compete favorably.

Figure 3.8 on p. 29 shows representative strategies for various values of the competition coefficients. It is significant that even a sixteen times return on investment for β is enough to markedly depress yields. The effect of α is less pronounced, but still significant. It is clear that in comparison with the effects of metabolism shown in Figure 3.6 on p. 24, competition has a much greater effect on the plant's yields and, thereby, its strategies.

Figure 3.9 on p. 30 shows a parameter sweep over various values of the competition coef-

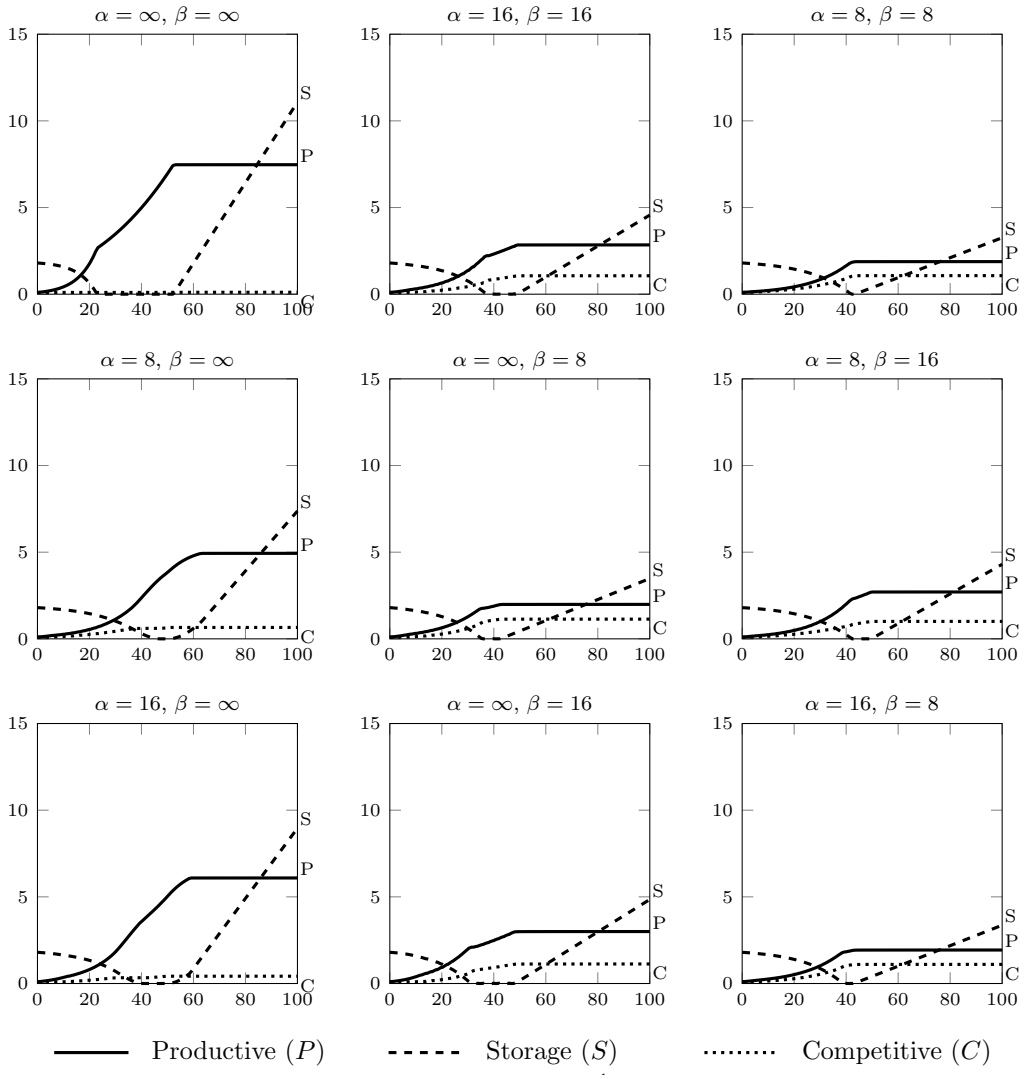

Figure 3.8: Representative strategies for plants in growing seasons of length $T = 100$ for the model with competition. The upper left graph, with no new variables included, is the same as is shown in the middle panel of Figure 3.6 on p. 24, where only metabolic costs are included. For ease of interpretation, each line is labeled with its corresponding variable at the edge of each subgraph as well as in the legend. $\mu_p = 0.005$ in all cases.

ficients for $\alpha = \beta$ with production metabolism set at $\mu_p = 0.005$ for a growing season of length $T = 120$. In the intense competition of a natural environment (low values of α and β), perennials would yield at considerably lower levels than replanted annuals in relatively less competitive environments. For the same level of competition, herbaceous perennials still yield lower than annuals, though it may be that seed size disparities or the economic

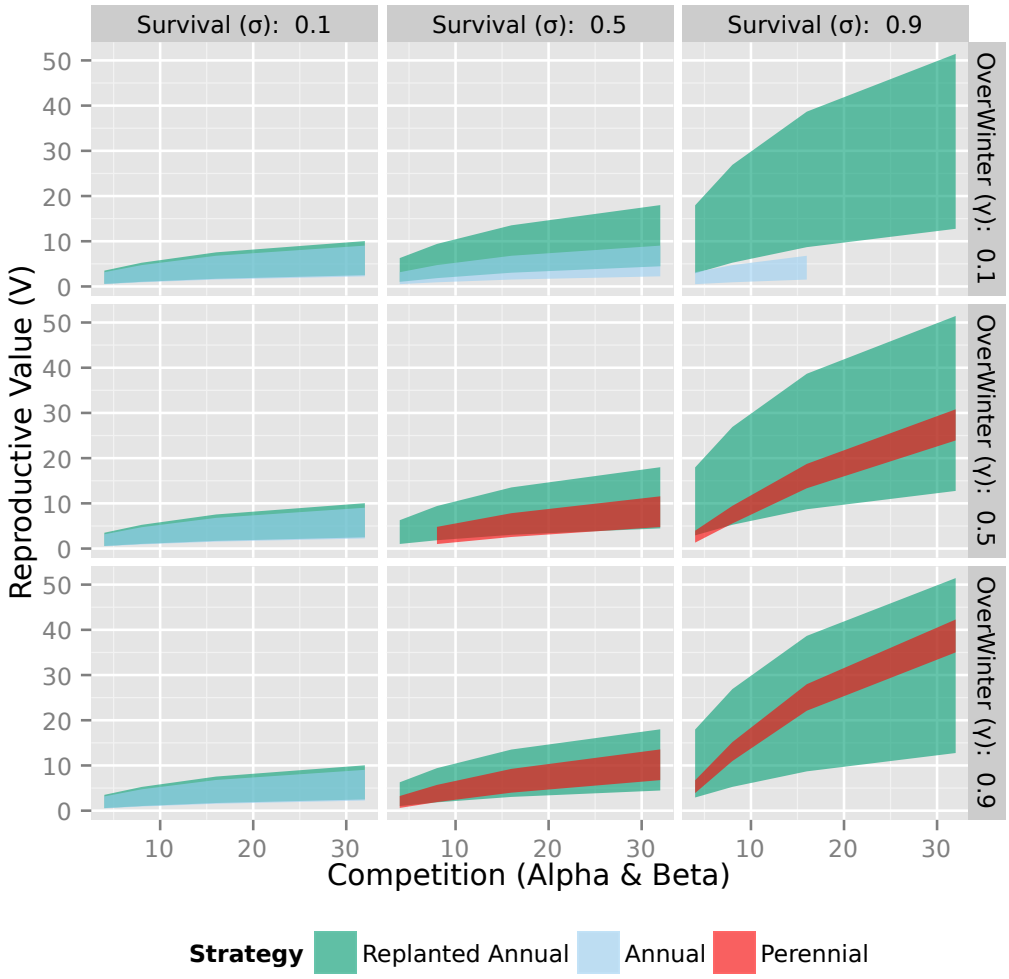

Figure 3.9: A parameter sweep across varying degrees of competition for $T = 120$, $\mu_p = 0.005$, $\alpha = \beta$, and $n = 8$. The spread indicates reproductive values for all initial seed masses ≤ 2. Lower values of α and β correspond to greater competition.

advantages of using perennials would be enough to offset this.

Chapter 4

Coda

4.1 Responses to possible objections

Some possible critiques of the foregoing model, modifications that could address them, and the probable results are as follows.

Leaves and fine roots provide different resources at different rates; this prevents them from being grouped into a single state variable. Iwasa and Roughgarden [33] and Iwasa [29] consider the situation in which a plant's moisture and light requirements are not equivalent. In this case, different amounts of roots and shoots will be required to form photosynthate. The growth equation used is

$$g(X_1, X_2) = \frac{1}{(a_1/L{X_1}^{b_1}) + (a_2/L{X_2}^{b_2})} \tag{4.1}$$

where X_1 is the leaf mass, L is the light intensity, X_2 is the fine root mass, and W is the soil moisture. In this system, allocation to the limiting organ is increased until a stoichiometric balance is achieved; that is, until the marginal return on investment for the two organs is the same. At this point allocation changes so that the two organs grow in synchrony. The results are, visually, very similar to those shown in Figure 3.8 on p. 29 for competitive tissue with the exception that, since both tissues are productive final storage values are not as depressed. Synchrony usually occurs early in the modeled growth of the plant after which the two state variables effectively function as a single state variable with a modified production rate. This suggests that using a single state variable to encompass both systems is permissible if the model is parameterized correctly. Since synchrony is achieved early on, the single-season model will likely produce results similar to those shown here, with

the limiting nutrient moderating growth. The behavior described here has been referred to elsewhere as the "equal limitation hypothesis". [64]

Leaves and fine roots have different nutrient requirements during construction that prevent them from being grouped into a single state variable. The previous point discusses how roots and leaves can be broken into separate compartments to capture different resources. A similar strategy could be used to represent different construction costs. The model must have two distinct essential resources, otherwise the plant would simply leave the more expensive organ ungrown. Therefore, growth will proceed until synchrony is reached and then proceed at a rate which is limited either by the limiting resource or the cost of constructing the more expensive organ.

Using a continuous-discrete hybrid model prevents a proper accounting of when growth is initiated and ended in a season, which prevents the exploration of a whole class of strategies. This critique is especially true in agricultural settings where spring rains may leave fields too wet for planting until months after natural systems have initiated growth, and early harvests prevent the acquisition of resources in the late summer and fall. Agricultural perennials would have access to longer growing seasons because they do not require replanting in the spring, so growth can initiate immediately, and because they survive into and past the fall.

The best response to this critique is to point out that the models used here demonstrate that perennials can yield at levels near to that of annuals even without the added advantage of accessing a longer growing season. Therefore, extending the growing season can only weight the odds in the perennial's favor.

However, to address related limitations, Mironchenko and Kozłowski [46] have recently introduced a continuous time control problem specified by the following system:

$$\dot{P} = u_2(t)g(S) - \mu_p(t)P \tag{4.2}$$

$$\dot{R} = \big(u_1(t) - u_2(t)\big)\, g(S) \tag{4.3}$$

$$\dot{S} = p_e(t)p_r(P) - u_1(t)g(S) - \mu_s(t)S \tag{4.4}$$

$$0 \leq u_1 \leq 1 \tag{4.5}$$

$$0 \leq u_2 \leq u_1 \tag{4.6}$$

$$S \geq 0 \tag{4.7}$$

$$R \geq 0 \tag{4.8}$$

$$P \geq 0 \tag{4.9}$$

where t is the time in a plant's life, P is the mass of productive tissue, R is the mass of reproductive tissue, S is the storage mass, u_1 is a control constrained to the range $[0, 1]$, u_2 is a control constrained by $[0, u_1]$, $p_r(P)$ is a self-limiting production rate, $g(S)$ controls the

growth of reproductive tissue, $p_e(t)$ is a seasonally-varying photosynthetic efficiency, and $\mu_s(t), \mu_p(t)$ are the seasonally-varying tissue loss rates of storage and production tissues, respectively. The following environmental equations are used to fill in the model.

$$p_r(P) = \frac{aP}{bP + k} \tag{4.10}$$

$$g(S) = cS \tag{4.11}$$

$$p_e(t) = 0.2 + 0.8 \left| \sin\left(\frac{\pi}{12} t\right) \right| \tag{4.12}$$

$$\mu_p(t) = d \left| \cos\left(\frac{\pi}{12} t\right) \right| \tag{4.13}$$

$$\mu_s(t) = e \tag{4.14}$$

where the variables a, b, c, d, e are varied to model different environments. By adjusting the amplitude and timing of tissue loss and photosynthetic efficiency, it is possible to simulate seasonality. By adjusting variables *a*-*e*, the authors show that the model can express annual, perennial, and biennial life strategies. The results they achieve are similar to my own early work using genetic algorithms to model multi-season life strategies. However, as was the case with my own work, this added expressiveness comes at the cost of considerable complexity. Nonetheless, in future work I may see whether it is possible to make use of such a formulation to address issues of season length. This could be of interest in determining the possible range limits of high-yielding perennials. My own approach would likely differ from that presented by Mironchenko and Kozłowski. While varying photosynthetic efficiency may induce seasonal behavior, the costs of making poor growth decisions in frost-prone environments can be enormous: I suspect that costs such as these drive growth strategies more than early-season resource availability.

Herbivory by insects and animals represents an unpredictable and high cost to plants, especially in settings in which continual occupation by a perennial of several years facilitates the growth of high populations of specialists. In agricultural settings strong efforts are made to shield plants from insects and the risk of insects is also borne by annuals which may be replanted in the same area year after year, so this is unlikely to affect my conclusions.

The problem of herbivory and unpredictable tissue loss has been considered by Denholm [19], Iwasa and Kubo [32], King and Roughgarden [36], and Klinkhamer, Kubo, and Iwasa [37]. A few general results emerge: (a) herbivory may induce a plant to have multiple switches between vegetative and reproductive growth as it works to recover from tissue loss, (b) excess productive tissue may be produced if loss is sufficiently predictable (as discussed here in §3.5 on p. 22), and (c) a plant may use storage tissue to recover from tissue losses, leading to earlier and larger investments in storage than would otherwise be the case.

Variation in the length of growing seasons induced by seasonal variation in sunlight, precipitation, or frost risk may inhibit the perennial strategy. This problem is considered for a single growing season by Amir and Cohen [2], Iwasa [30], and King and Roughgarden [35]. Iwasa summarizes the findings in the title of his paper "Pessimistic Plant". The optimal plant functionally behaves as though the growing season is shorter and resources less plentiful than is actually the case and, in good years, can benefit from excesses if it has sufficient phenotypic plasticity. The practical effect of this is that in situations where a perennial has access to a longer growing season than an annual, it will plan for a season that is more akin to that which the annual experiences than would otherwise be the case. Since the models developed here show that perennials can have yields near to that of annuals even for seasons of identical length, introducing this complexity would not change my conclusions.

Plants can withdraw some resources from tissues which they do not expect to survive and reallocate these resources to reproductive tissues, thereby bolstering yield. This is true, but it does not affect my conclusions since this strategy could be employed equally by both perennials and annuals to bolster end of season storage.

4.2 Conclusions

Using the foregoing, I am now able to address some of the hypotheses presented earlier.

Longevity may be energetically expensive thereby forcing perennials into low-yield states. The cost of longevity in this model arises from the delay in reproduction coupled with discounting. This cost is not sufficient to prevent perennials from yielding highly in minimally competitive environments. A factor not considered here is imperfect conversions to and from storage, which would represent an additional cost. However, conversion costs are likely to be relatively low since there would be strong evolutionary pressure to optimize conversion systems and, given that perennials yield at annual levels even in the presence of strong competition, storage costs are unlikely to make perenniality unfeasible in environments with low competition.

High yield levels may be offset by low levels of yield during establishment. Figure 3.5 on p. 21 provides some insight into this question. For favorable environments, even very short planning horizons produce yield levels that are about the same for perennials and replanted annuals. For less favorable environments the annuals may do better.

Perenniality in herbaceous plants is more expensive than in woody plants such that herbaceous perennials will never out-yield herbaceous annuals. A possibility not considered here is whether a plant could retain its competitive tissue (such as its stem) from year to year. Were this the case, the development of competitive tissue would be only a transient cost,

thereby permitting much greater growth in subsequent years. Some perennials have adopted this strategy to great success: palm nuts and sugarcane, both perennials, are two of the most productive plants in terms of calories per acre. Insofar as herbaceous perennials cannot save competitive tissue, perenniality is more expensive for them than it is for woody plants.

This model also addresses a broader debate in ecology. Cole [13] posed a demographic issue in which even a small fecundity advantage in a semelparous species would favor the evolution of semelparity over iteroparity. Charnov and Schaffer [8] later showed that if off-spring mortality is considered then iteroparity can be advantageous, a result which was generalized by Young [72]. This model suggests an alternative explanation for the evolution of iteroparity, which is that there exist environments wherein a plant which delays reproduction in favor of developing large vegetative or storage organs is able to produce sufficient off-spring in the future to offset the delay.

Given the above, the yield disparity which arises from comparing replanted annuals in low-competition agricultural environments against herbaceous perennials in high-competition natural environments is expected. In environments with similar competition, my models predict that herbaceous perennials should yield similarly to replanted annuals. If the perennials are given access to a longer growing season, my models predict that the perennials can out-yield the annuals.

Therefore, one of the dominant patterns of nature and civilization arises not from any physical constraint, but from contingency and interaction. Wielding these same tools and sufficient patience, these models predict that it is possible for our society to design a new form of agricultural crop—one that may support not just our society, but the longevity of our planet.

Chapter 5

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Appendix A

JModelica Environment Set-up

As of 02015-08-16, the following instructions produced a working version of JModelica on Lubuntu 15.04. The computer I compiled JModelica on had 8GB of RAM. When I tested this on a computer with 2GB of RAM, it did not work. I was working with a remote, console-only machine; hence, the use of `screen`.

Update the package list

```
sudo apt-get update
```

Download and install `screen`, so you can work quickly, and `subversion`, so you can start downloading stuff

```
sudo apt-get -y install screen subversion
```

Run screen with automatic logging, so the setup is reproducible

```
screen -L
```

Download and install the required packages

```
sudo apt-get -y install g++ gfortran ipython cmake swig           \
                        ant python-dev python-numpy python-scipy  \
                        python-matplotlib cython python-lxml      \
                        python-nose python-jpype libzip-dev       \
                        openjdk-7-jdk libboost-dev jcc pkg-config
```

I have modified the JModelica required packages to include:

- `openjdk-7-jdk` - this is used instead of JModelica's recommended openjdk-6-jdk.
- `libzip-dev` is necessary for JModelica as well.

- `libboost-dev` provisions `boost-flyweight`, which is needed to run `make casadi_interface`

Download JModelica on one screen. Revision 7885 is known to work with these instructions.

```
svn co https://svn.jmodelica.org/trunk@7885 JModelica.org
```

While IPOPT is available as a pre-compiled package for Ubuntu, it is recommended to build IPOPT from sources. The IPOPT packages provided for Ubuntu have had flaws (including the version provided for Ubuntu 12.04) that prevented usage with JModelica.org. Also, compiling IPOPT from sources is required when using the linear solvers MA27 or MA57 from the HSL library, since these are not available as open source software.

Get IPOPT on another screen

```
wget http://www.coin-or.org/download/source/Ipopt/Ipopt-3.12.4.tgz
```

Unpack IPOPT

```
tar xvzf Ipopt-3.12.4.tgz
```

Get IPOPT third-party packages

```
cd ~/Ipopt-3.12.4/ThirdParty/Blas
./get.Blas
cd ../Lapack
./get.Lapack
cd ../Mumps
./get.Mumps
cd ../Metis
./get.Metis
cd ../../                          #Go back to the IPOPT base dir
```

If you have access to the HSL codes MA57 or MA27 (you'll need to fetch them from `http://www.hsl.rl.ac.uk/ipopt/`) you'll want to install them. I had them on my local machine and was installing to a server, so I used `scp` to move them over

```
scp -C coinhsl-2014.01.10.tar.gz root@IP_ADDRESS:~/
```

Unpack the archive and move the contents to a place where IPOPT will see them

```
cd ~/Ipopt-3.12.4/ThirdParty/HSL
tar xvzf ~/coinhsl-2014.01.10.tar.gz
mv coinhsl-2014.01.10 coinhsl
```

Compile IPOPT

```
cd ~/Ipopt-3.12.4/
mkdir build
cd build
../configure
make -j 4                          #Compile using 4 cores (if you have them)
make install
```

Hopefully JModelica is done downloading by now.

Compile JModelica

```
cd ~/JModelica.org
mkdir build
cd build
../configure --with-ipopt=$HOME/Ipopt-3.12.4/build
make
make install
make install_casadi
```

Depending on how you have your Java set up, you may need to set up some environment variables as follows. That should not be necessary for the process described here, since you have installed the correct version of Java and set up expected paths. Nonetheless, if things don't work, the following may be of use.

```
export JAVA_HOME=/usr/lib/jvm/java-1.8.0-openjdk-amd64
export LD_LIBRARY_PATH="$JAVA_HOME/jre/lib/amd64/server:$LD_LIBRARY_PATH"
```

Once you have the paths set up, finish installing.

```
make install casadi_interface
```

It should be working!

But probably it isn't. When I did the above process, IPOPT did not find HSL, even though it was supposed to be baked in. If you get complaints about `libhsl.so` being missing try the following first, then look below for another important debugging step.

```
cd ~
tar xvzf coinhsl-2014.01.10.tar.gz
cd coinhsl-2014.01.10
./configure LIBS="-llapack" --with-blas="-L/usr/lib -lblas"      \
            CXXFLAGS="-g -O2 -fopenmp" FCFLAGS="-g -O2 -fopenmp" \
            CFLAGS="-g -O2 -fopenmp"
make -j 4
make install
```

The library will be installed to `/usr/local/lib`, but IPOPT won't detect it because it will have the wrong name. Fix that:

```
ln -s /usr/local/lib/libcoinhsl.so /usr/local/lib/libhsl.so
```

And IPOPT *still* won't detect it because you need to set `LD_LIBRARY_PATH`:

```
export LD_LIBRARY_PATH="/usr/local/lib:$LD_LIBRARY_PATH"
```

You can check on your dynamically loading libraries with `ldconfig -v`.

HSL will run with a single core unless you set the OpenMP environmental variable:

```
export OMP_NUM_THREADS=7 #or the number of cores you want to use
```

A.1 Compilation & Execution Issues

If you get the message

```
ImportError: cannot import name transfer_optimization_problem
```

You didn't run `make install casadi_interface`.

If you get the message

```
Tried to obtain MA27 from shared library "libhsl.so", but the following error occurred:
/usr/local/lib/libhsl.so: undefined symbol: dtrsm_
```

This is probably because you just ran `./configure` when you compiled HSL. Use this instead:

```
./configure LIBS="-llapack" --with-blas="-L/usr/lib -lblas"      \
            CXXFLAGS="-g -O2 -fopenmp" FCFLAGS="-g -O2 -fopenmp"
```

When running a script with `jm_python.sh` you get the message:

```
Exception of type: OPTION_INVALID in file
"../../../../Ipopt/src/Algorithm/IpAlgBuilder.cpp"
at line 321:
Exception message: Selected linear solver MA27 not available.
Tried to obtain MA27 from shared library "libhsl.so", but the following error occured:
libhsl.so: cannot open shared object file: No such file or directory
```

and it won't go away.

This is because the folks at JModelica decided to overwrite the `LD_LIBRARY_PATH` variable, rather than to append to it as is standard (I got the authors to fix this in Revision 7984). Go into `jm_python.sh` and edit the line

```
LD_LIBRARY_PATH=:/root/Ipopt-3.12.4/build/lib/: \
/usr/local/jmodelica/ThirdParty/Sundials/lib:   \
/usr/local/jmodelica/ThirdParty/CasADi/lib
```

to read

```
LD_LIBRARY_PATH=$LD_LIBRARY_PATH:/root/Ipopt-3.12.4/build/lib/: \
/usr/local/jmodelica/ThirdParty/Sundials/lib:                   \
/usr/local/jmodelica/ThirdParty/CasADi/lib
```

Appendix B

Code Documentation

Calculations exploring the model were performed using JModelica, Python, and C++. JModelica (§A) was used to perform optimal control calculations within a single season. Python was used to perform parameter sweeps and handle outputs and error logging. C++ was used to find optimal multi-year strategies using a Bellman-Ford approach.

B.1 Single-season simple model

The Modelica source for the single-season simple model described in §3.2 on p. 14 is as follows:

```
//The simple model, without metabolism, tissue loss, or competition.
optimization SimpleModel(objective=-S(finalTime), startTime=0, finalTime=100)
  parameter Real P0       = 0.1  "Productive Mass";
  parameter Real Snominal = 2.0;
  parameter Real S0       = Snominal-P0 "Storage Mass";

  parameter Real kP = 20;
  parameter Real a  = 0.1;

  //Fixed=true implies that the initial value must be what it is; otherwise, the
  //initial value would be taken as a guess.
  output Real P(start=P0, fixed=true, min=0, max=100);
  output Real S(start=S0, fixed=true, min=0, max=100);

  input Real u(min=0, max=1);
  input Real w(min=0, max=1);
equation
  der(P) = P/(kP+P)*u    +w*a*P;
  der(S) = P/(kP+P)*(1-u)-w*a*P;
end SimpleModel;
```

B.2 Single-season model with metabolism

The Modelica source for the single-season model with metabolism and tissue loss described in §3.5 on p. 22 is as follows:

```
optimization MetaModel(objective=-S(finalTime), startTime=0, finalTime=120)
  parameter Real Snominal = 2.0;
  parameter Real P0       = 0.1         "Productive Mass";
  parameter Real S0       = Snominal-P0 "Storage Mass";

  parameter Real kP = 20;
  parameter Real a  = 0.1;
  parameter Real mp = 0.02;
  parameter Real ms = 0.02;
  parameter Real lp = 0.02;

  //Fixed=true implies that the initial value must be what it is; otherwise, the
  //initial value would be taken as a guess.
  output Real P(start=P0, fixed=true, min=0, max=100, unit="kg");
  output Real S(start=S0, fixed=true, min=0, max=100, unit="kg");

  input Real u(min=0, max=1);
equation
  der(P) = P/(kP+P)*u    +u*a*P-lp*P;
  der(S) = P/(kP+P)*(1-u)-u*a*P-ms*S-mp*P;
end MetaModel;
```

B.3 Single-season model with competition

The Modelica source for the single-season model with competition described in §3.6 on p. 26 is as follows:

```
function growth
  input  Real P;
  input  Real kP;
  input  Real beta;
  input  Real C;
  input  Real mp;
  output Real dg;
algorithm
  dg := P/(kP+P)*(1-P/beta/C)-mp*P;
end growth;

function modu
  input  Real u;
  input  Real P;
  input  Real alpha;
```

```
    input  Real C;
    output Real uprime;
  algorithm
    uprime := u*(1-P/alpha/C);
  end modu;

  optimization CompetModel(objective=-S(finalTime), startTime=0, finalTime=100)
    parameter Real Snominal = 2        "Storage Mass";
    parameter Real P0 = 0.1            "Productive Mass";
    parameter Real C0 = 0.1            "Competitive Mass";
    parameter Real S0 = Snominal-P0-C0 "Storage Mass";

    parameter Real kP    = 20;
    parameter Real a     = 0.1;
    parameter Real alpha = 8;
    parameter Real beta  = 50000;
    parameter Real mp    = 0.005;

    //Fixed=true implies that the initial value must be what it is; otherwise, the
    //initial value would be taken as a guess.
    output Real P(start=P0, fixed=true, min=0, max=100);
    output Real S(start=S0, fixed=true, min=0, max=100);
    output Real C(start=C0, fixed=true, min=0, max=100);

    input Real u(min=0, max=1);
    input Real w(min=0, max=1);
  equation
    der(P) = (growth(P,kP,beta,C,mp) +a*P)*modu(u,P,alpha,C);
    der(S) =  growth(P,kP,beta,C,mp) *(1-modu(u,P,alpha,C)-w)-a*P*modu(u,P,alpha,C)-w*a*C;
    der(C) = (growth(P,kP,beta,C,mp) +a*C)*w;
  constraint
    u+w<=1;
  end CompetModel;
```

B.4 Interseasonal Model Parameter Sweep

The following Python script is used to run a parameter sweep over the simple single-season model. The runs are parallelized across a computer's cores and the results are collected in an SQLite3 database. Since this code is so similar between the different models considered, I only include the version used for the simple model. Translating this to account for metabolism and competition is a simple matter of adding additional variables to the sweep and the recording.

```
#!/usr/bin/env jm_python.sh
import itertools
import multiprocessing
import numpy as np
```

```
5  import sys
6  import signal
7  import os
8  import random
9  import sqlite3
10
11 def RunIwasa(params):
12   proc_output = open('stdout_'+str(os.getpid())+'.txt', 'a')
13   sys.stdout  = proc_output
14   sys.stderr  = proc_output
15
16   T        = params[0]
17   Snominal = params[1]
18   P0       = 0.1
19   a        = 0.1
20   kP       = 20
21
22   import pyjmi
23   signal.signal(signal.SIGINT, signal.SIG_IGN)
24
25   op = pyjmi.transfer_optimization_problem("SimpleModel", "model_simple.mop")
26
27   op.set('finalTime', T)
28   op.set('Snominal',  Snominal)
29   op.set('P0',        P0)
30   op.set('a',         a)
31   op.set('kP',        kP)
32
33   #op.setOption("print_time",False)
34
35   # Set options, see: http://www.jmodelica.org/api-docs/usersguide/1.13.0/ch07s06.html
36   opt_opts                                  = op.optimize_options()
37   opt_opts['n_e']                           = 50
38   opt_opts['IPOPT_options']['tol']          = 1e-5
39   opt_opts['result_file_name']              = '/tmp/jmopt_'+str(os.getpid())+'.dat'
40   opt_opts['IPOPT_options']['print_time']   = False
41   opt_opts['IPOPT_options']['print_level']  = 0
42   #opt_opts['IPOPT_options']['output_file']  = '/z/err_'+str(T)+'_'+str(So)+'_info.dat'
43   #See: http://www.coin-or.org/Ipopt/documentation/node50.html
44   opt_opts['IPOPT_options']['linear_solver'] = 'ma27'
45
46   res = op.optimize(options=opt_opts)
47
48   return (P0,Snominal,kP,a,T,res['S'][-1],res['P'][-1])
49
50 conn = sqlite3.connect('single_season.db')
51 c    = conn.cursor()
52
53 try:
```

```
    c.execute('''CREATE TABLE barnes_single (
      P0       real,
      Snominal real,
      kP       real,
      a        real,
      T        real,
      Sfinal   real,
      Pfinal   real
    )''')
    conn.commit()
  except sqlite3.OperationalError:
    pass

  T        = map(float,[10,20,30,40,50,60,70,80,90,100,110,120,130,140])
  Snominal = np.arange(0.1,30.1,0.1)
  tspairs  = list(itertools.product(T,Snominal))
  random.shuffle(tspairs)

  pool  = multiprocessing.Pool(maxtasksperchild=100)
  mapit = pool.imap_unordered(RunIwasa,tspairs)
  pool.close()

  completed = 0

  while True:
    try:
      res        = mapit.next(timeout=2)
      completed += 1

      c.execute("""INSERT INTO barnes_single
        (P0,Snominal,kP,a,T,Sfinal,Pfinal) VALUES (?,?,?,?,?,?,?)""",res)

      print "{0: >4} of {1: >4} ({2: >4} left)".format(
        completed,len(tspairs),len(tspairs)-completed)
    except KeyboardInterrupt:
      pool.terminate()
      pool.join()
      sys.exit(0)
    except multiprocessing.TimeoutError:
      print "{0: >4} of {1: >4} ({2: >4} left)".format(
        completed,len(tspairs),len(tspairs)-completed)
    except StopIteration:
      break

  conn.commit()
```

B.5 Finding a Multi-season Strategy

The following code uses dynamic programming to link the optimal single-season strategies together into an optimal multi-season strategy. It is very similar between the different models used.

```
//g++ -O3 -o multi_year_strat.exe 2_find_multi_year_strategy.cpp \
//         ../common/sqdb.cpp --std=c++11 -lsqlite3 -fopenmp
//https://code.google.com/p/sqdbcpp/
//TODO: See "https://github.com/SRombauts/SQLiteCpp"
#include <vector>
#include <iostream>
#include <iomanip>
#include <fstream>
#include <string>
#include <sstream>
#include <algorithm>
#include <cmath>
#include <cstdlib>
#include "../common/sqdb.h"
using namespace std;

typedef std::vector< std::vector <double> > values_t;
typedef std::vector< std::vector <int> > choices_t;
typedef std::vector<double> Svals;

template<class T>
void ResizeMatrix(std::vector< std::vector<T> > &vm, int t, int s0){
  vm.resize(t, std::vector<T>(s0,-1));
}

//Find the index of the largest number less than or equal to a needle number
size_t FindLargestLessThanEqualNeedleIdx(
  const std::vector<double> &v, //Sorted vector of values
  double needle                 //The target value
){
  auto up = std::upper_bound(v.begin(), v.end(), needle);
  if(up==v.begin())
    return 0;
  else if(up==v.end())
    return v.size()-1;
  else
    return up-v.begin()-1; //Pointer arithmetic
}

void OptimalPath(
  bool        replant, //Replant annuals
  double      sigma,   //Discount rate
```

```
    double      gamma,   //Over-winter loss
    const Svals &S0s,  //Initial storage masses (along with Sfs this is £\psi_T£)
    Svals       &Sfs,  //Optimal final storage masses (£\psi_T£)
    int         n,     //Number of years over which to optimize
    values_t    &values, //Matrix of reproductive values for each year
    choices_t   &choices //Matrix of optimal allocation choice for each year
  ){
    //'values' and 'choices' are two-dimensional matrices which cache
    //the reproductive value and optimal choices of subsequent years so
    //that they can be quickly looked up, rather than recalculated, in
    //the years which precede them. This turns an exponential
    //calculation O(n**len(Sfs)) into a O(n*len(Sfs)) problem.

    //If the initial storage is zero force the final storage to also be
    //zero. It may be slightly larger due to floating-point math.
    Sfs[0] = 0;

    //The final storage values represent the spectrum of possible
    //choices of storage to retain for a future year. We can
    //precalculate which cell on the horizontal (storage mass) axis of
    //the values matrix to look up for each possibility. Sf[s] is an
    //over-winter allocation, gamma*Sf[s] is the amount of that
    //allocation which survives the winter, FindLargest() is a function
    //which determines which initial storage mass is closest (but not
    //larger than) the amount which survived the winter. The final
    //storage mass associated with this is used in the Bellman equation.
    std::vector<int> PsiGammaS0(Sfs.size(),0);
    for(int s=0;s<Sfs.size();s++)
      PsiGammaS0[s] = FindLargestLessThanEqualNeedleIdx(S0s, gamma*Sfs[s]);

    //Work backwards in time from some future date to the present
    //determining the optimal values as we go.
    for(int t=n-1;t>=0;t--)
    for(int s=0;s<Sfs.size();s++){ //Consider each final storage size
      //These two variables define the optimal choice of storage mass to
      //save for the next season and the value of that choice. They are
      //initialized to dummy values that will be overwritten on the
      //first iteration of the loop.
      int bestchoice = -1;
      double bestval = -1;
      //All final storage sizes less than or equal to the current one
      //are candidates of storage that can be saved until the next
      //season. Consider them all unless replanting is activated, in
      //which case force a perennial strategy
      if(!replant){
        for(int skeep=0;skeep<=s;skeep++){
          //Determine the future value of the allocation choice. If this
          //is the final time, there is no future value at all; otherwise,
          //we fetch the cached future value.
```

```
92          double val = (t==n-1) ? 0 : sigma*values[t+1][PsiGammaS0[skeep]];
93          //Add to the future value the present value.
94          val += (Sfs[s]-Sfs[skeep]);
95          //If this is the best choice we've seen so far, make a note of it.
96          if(val>bestval){
97            bestval    = val;
98            bestchoice = skeep;
99          }
100       }
101     } else {
102       bestchoice = 0;
103       bestval    = (t == n-1) ? Sfs[s] : Sfs[s]+sigma*values[t+1][s];
104     }
105
106     //Cache the best choice and value for this time and initial
107     //storage value
108     values [t][s] = bestval;
109     choices[t][s] = bestchoice;
110   }
111 }
112
113 void GetSOSf(const char *dbfile, Svals &SOs, Svals &Sfs, double T){
114   sqdb::Db db(dbfile);
115   sqdb::Statement s = db.Query(
116       ("SELECT Snominal-P0 AS S0,Sfinal FROM barnes_single WHERE T="
117       +std::to_string(T)+" ORDER BY S0;").c_str());
118
119   while ( s.Next() ){
120     SOs.push_back(s.GetField(0));
121     Sfs.push_back(s.GetField(1));
122   }
123 }
124
125 void GetOptimal(
126   bool replant, const char *dbfile, double T,
127   double sigma, double gamma, int n, values_t &values, choices_t &choices
128 ){
129   Svals SOs, Sfs;
130   GetSOSf(dbfile, SOs, Sfs, T);
131   ResizeMatrix(values, n, SOs.size());
132   ResizeMatrix(choices, n, SOs.size());
133   OptimalPath(replant, sigma, gamma, SOs, Sfs, n, values, choices);
134 }
135
136 void ShowParticular(
137   bool replant, const char *dbfile, double T, double sigma,
138   double gamma, int n
139 ){
140   std::cout<<"T="<<T<<" sigma="<<sigma<<" gamma="<<gamma<<" n="<<n<<std::endl;
```

```
141
142     std::vector< std::vector<double> > values;
143     std::vector< std::vector<int> >    choices;
144     Svals SOs, Sfs;
145     GetSOSf(dbfile, SOs, Sfs, T);
146     GetOptimal(replant, dbfile, T, sigma, gamma, n, values, choices);
147
148     std::cout<<std::setw(10)<<"SO"<<std::setw(10)<<"Sf"<<std::endl;
149     for(int i=0;i<SOs.size();i++)
150       std::cout<<std::setw(10)<<SOs[i]<<std::setw(10)<<Sfs[i]<<std::endl;
151
152     double SO        = 2;
153     double total_val = 0;
154     double discount  = 1;
155     int idx          = FindLargestLessThanEqualNeedleIdx(SOs,SO);
156     std::cout<<SO<<" "<<T<<" "<<values[0][idx]<<std::endl;
157     for(int t=0;t<choices.size();t++){
158       double current_value = Sfs[idx] - Sfs[choices[t][idx]];
159
160       total_val += discount*current_value;
161       discount  *= sigma;
162
163       std::cout<<"SO="            <<std::setw(3)<<SOs[idx]
164                <<" Sf="           <<std::setw(7)<<Sfs[idx]
165                <<" Investment="   <<std::setw(7)<<Sfs[choices[t][idx]]
166                <<" Choice="       <<choices[t][idx]
167                <<" Value="        <<std::setw(7)<<values [t][idx]
168                <<" Current value="<<current_value
169                <<" Acc value="    <<total_val
170                <<std::endl;
171
172       idx = FindLargestLessThanEqualNeedleIdx(SOs, gamma*Sfs[choices[t][idx]]);
173     }
174
175     std::cout<<"Values"<<std::endl;
176     for(int s=0;s<SOs.size();s++)
177       std::cout<<std::setw(5)<<std::fixed<<std::setprecision(1)<<SOs[s]<<" ";
178     std::cout<<std::endl;
179
180     for(int t=0;t<values.size();t++){
181       for(int s=0;s<values[0].size();s++)
182         std::cout<<std::setw(5)<<std::fixed<<std::setprecision(1)<<values[t][s]<<" ";
183       std::cout<<std::endl;
184     }
185
186     std::cout<<"\n\n\nChoices"<<std::endl;
187     for(int t=0;t<choices.size();t++){
188       for(int s=0;s<choices[0].size();s++)
189         std::cout<<std::setw(5)<<choices[t][s]<<" ";
```

```
    std::cout<<std::endl;
  }
}



int main(int argc, char **argv){
  if(argc!=5){
    cout<<argv[0]<<" <Single Season data> <Output> <(no)replant> <n>"<<std::endl;
    return -1;
  }

  int n = std::stoi(argv[4]);

  Svals So_values;
  std::vector<double> T_values;
  sqdb::Db db(argv[1]);
  // Select all tuples from table t with two columns integer and float.
  sqdb::Statement s = db.Query(
    "SELECT DISTINCT Snominal-P0 AS a FROM barnes_single ORDER BY a;");
  while ( s.Next() )
    So_values.push_back(s.GetField(0));

  s = db.Query("SELECT DISTINCT T AS a FROM barnes_single ORDER BY a;");
  while ( s.Next() )
    T_values.push_back(s.GetField(0));

  //ShowParticular(true, argv[1], 100, 0.9, 0.9, 8);

  ofstream fout(argv[2]);
  fout<<"T          So       Sigma    Gamma    Rtot     ptype\n";
  #pragma omp parallel for collapse(3) //,  num_threads(8)
  for(unsigned int Ti=0;Ti<T_values.size();Ti++)
  for(int sigma_i=0;sigma_i<=10;sigma_i++)
  for(int gamma_i=0;gamma_i<=10;gamma_i++){
    double sigma = sigma_i*0.1;
    double gamma = gamma_i*0.1;

    std::vector< std::vector<double> > values;
    std::vector< std::vector<int> >    choices;
    GetOptimal(
      argv[3]==std::string("replant"),
      argv[1],
      T_values[Ti],
      sigma,
      gamma,
      n,
      values,
      choices
```

```
    );

    Svals SOs, Sfs;
    GetSOSf(argv[1], SOs, Sfs, T_values[Ti]);

    std::stringstream ss;
    for(int Si=0;Si<So_values.size();Si++){
       ss<<T_values[Ti]  <<" "
         <<So_values[Si] <<" "
         <<sigma         <<" "
         <<gamma         <<" "
         <<values[0][Si] <<" ";

        if(values[0][Si]<=So_values[Si]+0.1)
          ss<<"nogrowth";
        else if(choices[0][Si]==0)
          ss<<"annual";
        else
          ss<<"perennial";
        ss<<"\n";
         //<<Svallist[Si]<<" "
         //<<Svallist[Si]<<" "
        //<<"nogrowth"  <<"\n";
    }
    #pragma omp critical
    fout<<ss.str();
  }

  return 0;
}
```

B.6 Analysis

Graphs and statistics were generated with the following R script:

```
library(ggplot2)
library(dplyr)
library(RSQLite)
#require(grid)


laby<-function(var,val){
  if(var=="Sigma"){
    paste("Survival (σ): ",val)
  } else if(var=="Gamma"){
    paste("OverWinter (γ): ",val)
  } else if(var=="ptype"){
```

```
    paste("",val)
  }
}



readdata<-function(filename,n,all_annuals){
  msd<-read.table(filename,header=TRUE)
  msd<-data.frame(msd)
  #Clean up strategy names for display
  msd$ptype<-gsub("nogrowth","No Growth",
                  gsub("annual","Annual",
                       gsub("perennial","Perennial",msd$ptype)))

  msd$n<-n
  if(all_annuals){
    msd$ptype<-"Replanted Annual"
  }

  #Order strategy names as factors
  msd$ptype<-factor(msd$ptype,
    levels=c("Replanted Annual", "No Growth","Annual","Perennial"))

  #Extract data of interest
  subset(msd, (Gamma==0.1 | Gamma==0.5 | Gamma==0.9) &
              (Sigma==0.1 | Sigma==0.5 | Sigma==0.9) & So>0 & So<=2)
}

plotComp<-function(msd,outname){
  cairo_pdf(outname, width=6,height=6,family="DejaVu Sans")
  theme_set(theme_gray(base_size = 12))
  p<-ggplot(msd, aes(x=T,y=pmin(Rtot,70), fill=ptype))
  p<-p+ylab("Reproductive Value (V)")+xlab("Growing Season Duration (T)")
  p<-p+stat_summary(geom="ribbon", fun.ymin="min", fun.ymax="max", alpha=0.6)
  p<-p+scale_fill_manual(values=c("#009E73", "#e79f00", "#9ad0f3","red"))
  p<-p+guides(fill=guide_legend(title="Strategy"))
  p<-p+theme(legend.position="bottom")
  p<-p+facet_grid(Gamma~Sigma, labeller = laby)
  print(p)
  dev.off()
}

#What kinds of strategies dominant the parameter space of the simple model
msd<-readdata('iwasa_agg_multi_season8.dat',8,FALSE)
msd<-rbind(msd,readdata('iwasa_agg_multi_season8_annuals.dat',8,TRUE))
msd<-rbind(msd,readdata('iwasa_agg_multi_season4.dat',4,FALSE))
msd<-rbind(msd,readdata('iwasa_agg_multi_season4_annuals.dat',4,TRUE))
msd<-rbind(msd,readdata('iwasa_agg_multi_season2.dat',2,FALSE))
msd<-rbind(msd,readdata('iwasa_agg_multi_season2_annuals.dat',2,TRUE))
```

```
62
63  msd$ptype<-factor(msd$ptype, levels=c("Replanted Annual","No Growth","Annual","Perennial"))
64
65  plotComp(msd %>% filter(n==8),'strategy_yields8.pdf')
66
67  #How are these affected by the number of years over which we optimize?
68  smsd<-msd %>% filter(Gamma==0.9 & Sigma==0.9)
69  cairo_pdf("strategy_vary_n.pdf", width=6,height=4,family="DejaVu Sans")
70  theme_set(theme_gray(base_size = 12))
71  p<-ggplot(smsd, aes(x=T,y=pmin(Rtot,70), fill=ptype))
72  p<-p+ylab("Reproductive Value (V)")+xlab("Growing Season Duration (T)")
73  p<-p+stat_summary(geom="ribbon", fun.ymin="min", fun.ymax="max", alpha=0.6)
74  p<-p+scale_fill_manual(values=c("#009E73", "#e79f00", "red","red"))
75  p<-p+guides(fill=guide_legend(title="Strategy"))
76  p<-p+theme(legend.position="bottom")
77  p<-p+facet_grid(~n) #, labeller = laby)
78  print(p)
79  dev.off()
80
81
82  #What kinds of strategies dominate if metabolism is included?
83  msd<-readdata('model_meta/meta_multi_season8.dat',8,FALSE)
84  msd<-rbind(msd,readdata('model_meta/meta_multi_season8_annuals.dat',8,TRUE))
85  msd<-rbind(msd,readdata('model_meta/meta_multi_season4.dat',4,FALSE))
86  msd<-rbind(msd,readdata('model_meta/meta_multi_season4_annuals.dat',4,TRUE))
87  msd<-rbind(msd,readdata('model_meta/meta_multi_season2.dat',2,FALSE))
88  msd<-rbind(msd,readdata('model_meta/meta_multi_season2_annuals.dat',2,TRUE))
89
90  msd$ptype<-factor(msd$ptype, levels=c("Replanted Annual","No Growth","Annual","Perennial"))
91
92  plotComp(msd %>% filter(n==8),'model_meta/strategy_yields8.pdf')
93
94  #What kinds of strategies dominate if competition is included?
95  temp4 <-readdata('model_compet/compet_multi_season8_4.dat',8,FALSE)
96  temp4 <-rbind(temp4,readdata('model_compet/compet_multi_season8_annuals_4.dat',8,TRUE))
97  temp8 <-readdata('model_compet/compet_multi_season8_8.dat',8,FALSE)
98  temp8 <-rbind(temp8,readdata('model_compet/compet_multi_season8_annuals_8.dat',8,TRUE))
99  temp16<-readdata('model_compet/compet_multi_season8_16.dat',8,FALSE)
100 temp16<-rbind(temp16,readdata('model_compet/compet_multi_season8_annuals_16.dat',8,TRUE))
101 temp32<-readdata('model_compet/compet_multi_season8_32.dat',8,FALSE)
102 temp32<-rbind(temp32,readdata('model_compet/compet_multi_season8_annuals_32.dat',8,TRUE))
103 temp4$alpha<-4
104 temp4$beta <-4
105 temp8$alpha<-8
106 temp8$beta <-8
107 temp16$alpha<-16
108 temp16$beta <-16
109 temp32$alpha<-32
110 temp32$beta <-32
```

```
msd<-rbind(temp4,temp8,temp16,temp32)

msd$ptype<-factor(msd$ptype, levels=c("Replanted Annual","No Growth","Annual","Perennial"))


#How do things vary for all blocks with alpha if we consider only a single T
smsd<-msd %>% filter(n==8 & T==120)
cairo_pdf("model_compet/strategy_vary_alpha_allT.pdf", width=6,height=6,
  family="DejaVu Sans")
theme_set(theme_gray(base_size = 12))
p<-ggplot(smsd, aes(x=alpha,y=pmin(Rtot,70), fill=ptype))
p<-p+ylab("Reproductive Value (V)")+xlab("Competition (Alpha & Beta)")
p<-p+stat_summary(geom="ribbon", fun.ymin="min", fun.ymax="max", alpha=0.6)
p<-p+scale_fill_manual(values=c("#009E73", "#9ad0f3", "red","red"))
p<-p+guides(fill=guide_legend(title="Strategy"))
p<-p+theme(legend.position="bottom")
p<-p+facet_grid(Gamma~Sigma, labeller = laby)
print(p)
dev.off()









#Plot figure 4 from Iwasa 1989
ss<-read.csv('iwasa_agg_single_season.dat',sep=" ",header=TRUE)
colnames(ss)
ss<-data.frame(ss)
sp<-ss
sp<-subset(ss, T==50)# | T==30 | T==50)
sp$T<-factor(sp$T)
p<-ggplot(sp,aes(x=So,y=Sf,color=T))+geom_line(size=2)#+xlim(c(0,2.5))+ylim(c(0,14))
p<-p+xlim(0,40)+ylim(0,30)
p<- p + geom_abline(intercept=0, slope=1)
p

#Plot Figure 5 from Iwasa 1989
dsub<-subset(d,Gamma==0.8)                        #Subset data along the Gamma axis
p<- ggplot(dsub,aes(x=T,y=Sigma,color=Sof/Sff))  #Build plot along appropriate axes
p<- p + geom_point(alpha=0.3)                     #Use points to represent data
p<- p + geom_jitter()                             #Jitter the points so they don't overlap
p<- p + facet_grid(~ptype)                        #Break into 3 plots split on ptype
p<- p + guides(fill=guide_legend(title="So/Sf")) #Label z axis
```

```
p<- p + scale_x_continuous(expand=c(0,0))         #Expand view to limiting axes
p<- p + scale_y_continuous(expand=c(0,0))         #Expand view to limiting axes
p

p<-p+scale_fill_brewer(type="seq",palette = "YlGn")



temp<-msd %>% filter(Sigma==0.9 & Gamma==0.3) %>% mutate(reff=Rtot/(S))
p <- ggplot(temp) + geom_point(aes(x=T,y=reff,color=So))
p



#What does the function Psi look like for the simple model?
cairo_pdf("model_simple/psi.pdf", width=3,height=3,family="DejaVu Sans")
con  <- dbConnect(SQLite(), "model_simple/single_season.db")
temp <- dbGetQuery(conn=con, statement="SELECT * FROM barnes_single WHERE T%20=0")
temp$T <- factor(temp$T)
p<-ggplot(temp)+geom_line(aes(x=(Snominal-P0),y=Sfinal,colour=T),size=1)
p<-p+xlim(0,10)+ylim(0,45)
p<-p+xlab("Initial Storage Mass (S0)")+ylab("Final Storage Mass")
p<-p+guides(color=guide_legend(title="Season\nLength (T)"))
p<-p+theme(text = element_text(size = 10)) # this will change all text size
print(p)
dev.off()


#What does the function Psi look like if we include metabolism?
cairo_pdf("model_simple/psi.pdf", width=3,height=3,family="DejaVu Sans")
con  <- dbConnect(SQLite(), "model_meta/single_season.db")
temp <- dbGetQuery(conn=con,
  statement="SELECT * FROM barnes_single WHERE T%20=0 AND mp=0.01 AND ms=0 AND lp=0")
temp$T <- factor(temp$T)
p<-ggplot(temp)+geom_line(aes(x=(Snominal-P0),y=Sfinal,colour=T),size=1)
p<-p+xlim(0,10)+ylim(0,45)
p<-p+xlab("Initial Storage Mass (S0)")+ylab("Final Storage Mass")
p<-p+guides(color=guide_legend(title="Season\nLength (T)"))
p<-p+theme(text = element_text(size = 10)) # this will change all text size
print(p)
dev.off()







#Todo: Examples
#p <- p + theme(axis.text = element_text(size = 15)) # changes axis labels
#p <- p + theme(axis.title = element_text(size = 25)) # change axis titles
```